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Epidemiological studies of shading effects on Asian soybean rust

Ana Paula da Silva Dias
Iowa State University

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Epidemiological studies of shading effects on Asian soybean rust

by

Ana Paula da Silva Dias

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Plant Pathology

Program of Study Committee:
Xiao Bing Yang, Major Professor
William Gutowski
Mark Gleason
Gregory Tylka
Philip Dixon
Zaitao Pan

Iowa State University

Ames, Iowa

2008

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This study is dedicated to the Brazilian soybean growers who lost their lifetime savings to successive soybean rust outbreaks.

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LIST OF SYMBOLS

ASR: Asian soybean rust

t: time

Y_{Mn} : disease incidence in the monomolecular model at time $t = n$

Y_{M0} : disease incidence in the monomolecular model at time $t = 0$

r_M : monomolecular apparent infection rate

α : rate of change in apparent infection rates

$Y_{M<shade>}$: disease incidence in the monomolecular model in the shade at time $t = n$

$Y_{M<sunlight>}$: disease incidence in the monomolecular model in sunlight at time $t = n$

Y_{Ln} : disease incidence in the logistic model at time $t = n$

Y_{L0} : disease incidence in the logistic model at time $t = 0$

r_{Ln} : logistic apparent infection rate

SAWS: South Africa Weather Service

INMET: Instituto Nacional de Meteorologia

EMBRAPA: Empresa Brasileira de Pesquisa Agropecuária

USDA: United States Department of Agriculture

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ABSTRACT

Asian soybean rust (ASR), caused by the fungus *Phakopsora pachyrhizi*, is considered to be the most threatening disease in major soybean production regions worldwide. Leaf infection usually results in premature defoliation, which reduces soybean yield components related to pod number, seed number, and size. Among other environmental factors, sunlight intensity negatively affects *P. pachyrhizi* biology with possible effects on disease epidemiology. Field observations suggest that higher disease severity occurs in shaded environments, such as on soybean leaves in the lower canopy and kudzu leaves under trees, compared with open ground. In this thesis, investigations have been carried out with the following three objectives: 1) to experimentally quantify the effects of shade intensity and duration on ASR establishment on soybean; 2) to apply results from shading experiments to parameterize a simulation model for temporal disease development using seasonal cloud cover data; and 3) to characterize and compare the spatial and temporal patterns of regional disease movement in different soybean production regions/seasons and to analyze the impact of solar radiation intensity on spatial and temporal disease dynamics.

Results from 2005 to 2007 support field observations that ASR incidence and severity are greater in the shade compared with no shade. Inoculated soybean plants placed in the shade for at least 2 days had significantly greater disease incidence and severity compared with those without shade. From our experimental results, a simulation model was developed to estimate temporal disease progress regulated by cloud cover conditions. The model was validated with disease data from Brazil and South Africa with correlation coefficients greater than 0.9. On average, severe ASR epidemics developed when 18 cloudy days were observed

after disease onset, and mild epidemics occurred when only 8 cloudy days were observed. In four growing seasons in Brazil and two in the United States, the progress of Asian soybean rust epidemics did not follow a wavelike pattern, and it resulted in an exponential distribution of distances to disease locations over time with variable monthly expansion rates. The disease front reached 500 km distance from major inoculum sources after 3 months similarly in both countries. Greater solar radiation intensity was associated with delays in epidemic onset. This was the first study to investigate the effects of solar radiation on ASR development; our results may be useful to improve risk assessments for seasonal ASR epidemics.

CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

Introduction

Soybean rust is caused by two fungi: *Phakopsora meibomiae* and *P. pachyrhizi*. The former has been observed in South and Central America without causing severe damage to soybean (HARTMAN et al., 1999). *P. pachyrhizi* was originally reported in Asia and then in Australia; Africa; and South, North, and Central America (HARTMAN et al., 1999; KAWUKI et al., 2003; YORINORI et al., 2005; SCHNEIDER et al., 2005). Due to the pathogen's origin, the disease caused by *P. pachyrhizi* is called Asian soybean rust. Since *P. pachyrhizi* is the more aggressive of the two species, recent studies, including this thesis, have focused on Asian soybean rust. Hereafter, we will refer to Asian soybean rust as soybean rust.

Thesis organization

This thesis is organized in five main chapters. In this chapter, general aspects of the pathogen's biology and soybean rust epidemiology were reviewed and trends in recent research were addressed. In the second chapter, experimental studies on the effects of shading on soybean rust establishment were described and results were discussed for their relevance to current knowledge on soybean rust epidemiology. In the third chapter, a modeling approach was used to simulate soybean rust temporal progress on a regional scale using cloud cover to regulate apparent disease infection rates in Brazil and South Africa. In

the fourth chapter, locations and dates of soybean rust detections were analyzed in combination with solar radiation estimates to compare the disease's spatial patterns of front movements in Brazil and the United States. In the fifth chapter, the combined results from our research were analyzed to draw conclusions about Asian soybean rust epidemiology with respect to shading effects.

Disease overview

Geographic distribution and regional epidemics. For a long time, soybean rust was only in the Eastern Hemisphere, causing yield losses in some regions. From 1994 to 1998, among the top 10 soybean-producing regions only China and Indonesia reported yield losses due to soybean rust (WRATHER et al., 1997 and 2001). In the past decade, the disease was reported in other soybean-producing regions worldwide. In 1996, soybean yield losses were associated with outbreaks of soybean rust in Uganda and Kenya (KAWUKI et al., 2003). From these countries, the disease possibly expanded southwards to Rwanda, Zambia, and Zimbabwe during the following two years (LEVY, 2005). Soybean rust further expanded to South Africa by 2001 (PRETORIUS et al., 2001). Severe disease outbreaks have been reported in Zimbabwe and in KwaZulu-Natal Province, South Africa, resulting in moderate to severe yield losses (LEVY, 2005; E. DUPREEZ, personal communication). Fungicide trials, screening for host resistance, and cultural methods have been studied in southern Africa for soybean rust control (KAWUKI et al., 2003).

Soybean rust was detected for the first time in South America during the 2001 growing season in Paraguay. The disease quickly expanded to major soybean-producing areas in Brazil (YORINORI et al., 2005), Argentina (ROSSI, 2003), and Uruguay (STEWART et al., 2005). In Brazil, the disease caused frequent yield losses and a need for intensive fungicide applications (YORINORI and LAZZAROTTO, 2004). Early-season disease onset and severe epidemics have often been observed in Mato Grosso State where soybean is planted during the winter under irrigation (SIQUERI, 2005). The pathogen overwinters on winter soybean, and inoculum is likely to build up during the early season. Further, suitable weather conditions with frequent rainfall favor disease development in that region (Del PONTE et al., 2006). In some regions of Mato Grosso, although growers reportedly had to apply fungicide five times in 2004, yield losses were still observed (SIQUERI, 2005). Most soybean-producing states in Brazil have reported soybean rust outbreaks every year (EMBRAPA SOJA, 2007). However, epidemic intensities vary among regions and growing seasons. In most locations, disease epidemics have been moderate to mild, resulting from unfavorable weather conditions or late disease onset (GODOY et al., 2006; OLIVEIRA, 2005; BALARDIN et al., 2005; NUNES JR. et al., 2005; AZEVEDO, 2005; JULIATTI, 2005; ANDRADE, 2005).

In Argentina, soybean rust was first detected in 2002, and the disease has been observed in different provinces every year (IVANCOVICH, 2005; FORMENTO, 2007). The pathogen overwinters on volunteer soybean and kudzu (*Pueraria lobata*). Viable uredinospores are produced on these hosts after exposure to below-freezing temperatures for many days (FORMENTO and SOUZA, 2006). Similar to other temperate regions, the

patterns of disease expansion from overwintering regions to higher latitudes in Argentina and Uruguay usually occur during the late season, resulting in mild to moderate epidemics (CARMONA et al., 2005; STEWART, personal communication). In 2004, the majority of soybean rust detections were in March and April during soybean's late reproductive stages (FRIGIDI, 2005).

In 2004, soybean rust was detected for the first time in Colombia and then in the continental United States (NPDDN, 2004; SCHNEIDER et al., 2005). The disease rapidly expanded to south-central Florida and southwestern states where the pathogen is most likely to overwinter (USDA, 2007; PIVONIA and YANG, 2004). In 2005, the disease was found in northern soybean regions of Mexico next to potential overwintering regions in southern Texas (CÁRCAMO et al., 2005; USDA, 2007; PIVONIA and YANG, 2004). With the presence of *P. pachyrhizi* in the continental United States, the spread and intensity of soybean rust epidemics vary among three growing seasons. Overwintering regions in southern Florida and Texas are active since the initial disease detections were made near those areas during the growing season (USDA, 2007). In 2005 and 2006, soybean rust uredinospores were found as far north as North Dakota during the soybean growing season (KRUPA et al., 2006; BARNES and Szabo, 2007). However, the disease was observed during the late season in regions of high latitudes resulting in mild epidemics, similar to the patterns observed in Argentina and China (USDA, 2007; YANG, 2005; FRIGIDI, 2005). In 2007, the disease was reported for the first time in Canada (USDA, 2007).

Disease symptoms. The characteristic symptoms of soybean rust are small (2–5mm) green to brownish or red-brown lesions on leaflets where salient globose uredinia, commonly known

as pustules, emerge to produce uredinospores. There is no yellow halo around the lesions, but lesion types differ accordingly to host-pathogen compatibility. In compatible reactions, lesions are tan colored with few uredinia and no necrosis. In semitolerant reactions, lesions are dark reddish brown with some necrosis and, sometimes, without any uredinia (HARTMAN et al., 1999). In most cases, initial lesions can be observed 7 to 9 days after inoculation, and 2 days later uredinia emerge, mostly from the abaxial leaf surface. In severe cases, the lesions can be observed on stems and petioles (HARTMAN et al., 1999). Late in the season, telia develop on the uredinia as dark brown round structures, which can produce teliospores. Leaflets with more than 20% disease severity are likely to turn yellow, resulting in premature abscission (YANG et al., 1990).

To standardize the assessment of soybean rust development, disease severity scales have been proposed (BROMFIELD, 1984; GODOY et al., 2006). Estimation of disease incidence (proportion of diseased plants or diseased plant parts) is most suitable during early epidemic stages for rapidly expanding diseases such as soybean rust. Assessments of disease severity have been preferred especially in breeding programs and fungicide trials for soybean rust control. The most recent categorical severity scales can be statistically analyzed even in complex experimental designs (GODOY et al., 2006; SHAH and MADDEN, 2004).

In diagnosis, soybean rust is often confounded with other common soybean diseases, especially at early developmental stages before uredinia are formed. However, the prominent structures of the uredinia are unique to soybean rust. For disease diagnosis, leaflets with suspect lesions are usually incubated for a few hours to allow pustule emergence and

sporulation. Further diagnosis techniques include observation of uredinospores, serologic tests, and PCR analysis.

Pathogen biology and disease cycle. Similar to other rust pathogens, *P. pachyrhizi* is an obligate parasite depending on living hosts for survival and reproduction. For this pathogen, environmental conditions negatively affecting the host's survival can also decrease the ability of the pathogen to overwinter. At most tropical locations, there is no limitation on pathogen overwintering except for a few locations at higher elevations in western South America and some heat-stressed regions in Brazil and south-central Africa (PIVONIA and YANG, 2004). In the United States, *P. pachyrhizi* is likely to overwinter only in central and southern Florida and southern Texas (PIVONIA and YANG, 2004). Similarly, in southern areas of South America, *P. pachyrhizi* is unlikely to overwinter although subfreezing temperatures observed in 20 consecutive days did not limit fungal survival in Argentina (FORMENTO and SOUZA, 2006). In northern Florida, the pathogen has been found to survive on kudzu plants protected from low temperatures by tall plants and at construction sites (WRIGHT et al., 2006; JURICK et al., 2007). In recent studies the fungus survived on dry leaves at subfreezing temperatures for many weeks and viable uredinospores were recovered after leaf rehydration (W. JURICK, personal communication).

Reproduction of soybean rust can be active on living hosts for several days. Fourteen new uredinia may be formed on a unique soybean rust lesion in 6 weeks (MELCHING et al., 1979). Furthermore, one mature uredinium produces over 2000 uredinospores in 45 days (YEH et al., 1982). However, some specific environmental conditions reportedly affect formation and sporulation of soybean rust uredinia on infected leaves. Inoculated plants

incubated at temperature under 20°C had a longer latent period compared to plants incubated at 20 to 25°C (KEOGH, 1974; KOCHMAN, 1979). Usually, development of uredinia and uredinospore production are more frequent on abaxial leaf surfaces, which escape direct sunlight exposure, compared to the upper surfaces (MARCHETTI et al., 1975; MELCHING et al., 1979 and BROMFIELD et al., 1980).

Fresh uredinospores emerge from the uredinia and are carried by air currents for dispersal. Single, detached uredinospores are most frequently collected from infected kudzu leaves, but clumps of 4 to 30 spores have also been observed (LI et al., 2006). The aggregation of spores may reduce the distance of spore movement, but spore clumping probably protects the internal spores from desiccation (LI et al., 2006). Airborne soybean rust uredinospores are particularly sensitive to UV radiation. No spores survived direct solar radiation of 25 MJ m⁻² over 2 days (ISARD et al., 2006). Dry and wet deposition of wind-borne uredinospores is likely to occur when spores have been collected from rain gauges or from slide traps protected from rain drops (RUPE and WIGLESWORTH, 2005; BARNES and Szabo, 2007).

After landing on susceptible host tissue, uredinospores start germination in the presence of free moisture (MAGNANI et al., 2007; KOCHMAN, 1979). Germinating uredinospores strongly adhere to leaf surfaces one hour after inoculation (VÉLEZ-CLIMENT et al., 2006). In general, developing germ tubes can elongate up to 185 µm, although germ tubes usually exhibited reduced growth under light and negative phototropism in two independent studies (KEOGH, 1974; KOCH and HOPE, 1987). Six hours after initial germination, over half of germinated uredinospores develop appressoria (MAGNANI et al.,

2007; KOCHMAN, 1979; MCLEAN and BYTH, 1981; KOCH et al., 1983). Twelve hours after inoculation, some of the soybean rust appressoria become mature and the penetration process is initiated (KOCK et al., 1983). In the appressorium, a funnel-shaped structure, also called the appressorial cone, is formed and the penetration hypha develops (KOCK et al., 1983; MAGNANI et al., 2007). The penetration hypha directly penetrates the host's epidermal cell wall to reach the mesophyll where the fungal colonization begins. This process is usually completed 20 to 24 hours after inoculation (KOCK et al., 1983). Haustoria are fundamental structures for obligate parasites such as soybean rust fungus since they are responsible for fungal nourishing and maintenance of the parasitic relationship with host cells (AGRIOS, 2005). Few studies have successfully demonstrated formation of haustoria during soybean rust colonization due to the difficulties of staining colonizing hyphae. Initial formation of haustoria was observed 24 to 48 hours after inoculation (KOCH et al., 1983; MAGNANI et al., 2007; YANG, 1991). Five to seven days after soybean rust infection, the reproductive structures are formed and the disease cycle restarts. Uredinia are the most commonly observed and functional reproductive structures. Telia may be observed 40 days after incubation at a 17–22°C daily temperature cycle under high humidity (POOLPOL and PUPIPAT, 1985). Teliospores were recovered from randomly sampled infected leaves in Argentina and Florida (CARMONA et al., 2005; HARMON et al., 2007). Usually, teliospore germination is observed after several wetting cycles to form basidia and basidiospores (SAKSIRIRAT and HOPPE, 1991).

Host range. Unlike many other rusts, soybean rust has a large host range including many species in the Leguminosae family and other plant families (HEDGE et al., 2003; ONO

et al., 1992; BROMFIELD, 1984). Soybean (*Glycine max*) and kudzu (*Pueraria lobata*) are the most important hosts epidemiologically. Soybean is economically affected by the disease and kudzu is a common overwintering host. Common beans (*Phaseolus vulgaris*) and cowpea (*Vigna unguiculata*) are also important crops in some regions where the pathogen is present. However, the disease does not usually cause severe epidemics in these crops, and their importance for spore production in natural conditions is unclear. Recent breeding programs are attempting to incorporate resistance genes from alternative soybean rust hosts (PATZOLDT et al. 2007; HARTMAN et al., 2005; PASTOR-CORRALES et al., 2006).

Environmental conditions. *P. pachyrhizi* is affected by a range of environmental factors whose variation at a given location determines the severity of the epidemic. Uredinospore viability was reduced with exposure to temperatures above 28.5°C prior to germination (KOCHMAN, 1979). Higher infection rates were reported at 20 to 25°C compared to lower or higher temperature regimes after spores received at least 6 hours of dew (MARCHETTI et al., 1975). Leaf wetness is required for spore germination and infection. Spore germination often starts 2 to 4 hours after spores land on wet leaves, but a minimum period of 6 hours of dew is necessary for infection (KEOGH, 1974; MARCHETTI et al., 1975; MELCHING et al., 1989). However, the epidemiological importance of frequent dew periods is still unclear. Uninoculated soybean plants receiving spores from nearby sources in different dew period regimes, including 3-, 6-, or 9-day dry intervals between consecutive dew periods, had similar disease severity regardless of the dew frequency (MELCHING et al., 1989).

On a regional scale, frequent rainfall has been associated with severe soybean rust outbreaks. In a recent study, disease severity was highly correlated with rainfalls and number of rainy days in Brazil (Del PONTE et al., 2006). Similar observations were reported in China, where severe outbreaks occurred in years with rainfall above 200 mm or 12 rainy days per month for the months of September or October (TAN et al., 1996). The presence of clouds for prolonged periods should affect regional environmental conditions by stabilizing temperature variation and reducing direct solar radiation.

Growth of germinated spore tubes of soybean rust fungus was reportedly affected by light (KEOGH, 1974; KOCH and HOPPE, 1987). At different temperature regimes, higher spore germination rates were always observed when the germinating spores had 22 hours of darkness exposure compared to the ones in the dark for only 4 hours (MARCHETTI et al., 1975). In two independent studies, delayed light exposure or inhibited uredinospore germination reduced germ tube growth, and germ tubes exhibited negative phototropism (KEOGH, 1974; KOCH and HOPPE, 1987). The number of appressoria formed from germinated spores was higher in the dark compared to light conditions (KEOGH, 1974). The postpenetration processes of soybean rust fungus may also be affected by light. Increasing numbers of haustoria were formed when plants were maintained in the dark, but the haustoria formation rate declined when plants were brought back into the light (MCLEAN, 1979). More lesions were recovered from inoculated plants incubated at longer dark periods, although penetration rates were similar after 8 hours of darkness (BONDE et al., 1976). In general, fewer telia were observed when plants were exposed to high light intensity under similar temperature regimes (DUFRESNE et al., 1987).

Disease modeling. Latent periods from 10 to 14 days have been reported for different isolates of *P. pachyrhizi* on soybean (HARTMAN et al., 1999; BONDE et al., 2006; BURDON and MARSHALL, 1981). Longer latent periods were observed on alternative hosts and in unfavorable temperature conditions (BURDON and MARSHALL, 1981; KEOGH, 1974; KOCHMAN, 1979). Development of soybean rust epidemic relies on secondary infection cycles and the disease is classified as polycyclic (VANDERPLANK, 1963). The temporal development of soybean rust has been described mathematically by the logistic model with apparent infection rates from 0.05 to 0.27 in different years and locations (KAWUKI et al., 2003; TSCHANZ and WANG, 1980). Apparent disease infection rates are usually influenced by local environmental conditions (MADDEN et al., 2007). Soybean rust severity has been simulated using apparent infection rates estimated with a function that used night temperatures as a driving variable (KIM et al., 2005).

The most evident effect of soybean rust on soybean is the reduction in photosynthetic leaf area. In two studies using disease data from Taiwan, premature defoliation started at 20% disease severity leading to 10% mean yield losses (YANG et al., 1990; HARTMAN et al., 1991). Half of the foliage was lost at 60% disease severity resulting in yield losses between 40 and 60% compared to fungicide-protected plants (YANG et al., 1990; HARTMAN et al., 1991). The onset time of soybean rust at different soybean growth stages also affects crop yield components. The number and size of pods decreased on unprotected soybean plants inoculated at R1, R3, and R5 growth stages (HARTMAN et al., 1991). In addition, fewer and smaller seeds were produced (YANG et al., 1992; HARTMAN et al.,

1991; KAWUKI et al., 2003). Earlier inoculation resulted in greater yield reductions compared to plants inoculated at R5 (HARTMAN et al., 1991).

Some empirical and semi-empirical models have been developed to simulate soybean rust epidemic potential, temporal disease development, and disease impacts on soybean yield (YANG et al., 1991; YANG et al., 1992; BATCHELOR et al., 1997; REIS et al., 2004; KIM et al., 2005; Del PONTE et al., 2006). These models were based on established relationships between influential environmental variables and disease-crop development, which resulted in biologically meaningful estimates.

In the past, few studies were conducted on the spatial dynamics of soybean rust. Most studies reported the regional distribution of the disease over large countries such as China and Australia (TSCHANZ and SHANMUGASUNDARAM, 1984; STOVOLD and SMITH, 1991). However, these studies rarely applied concepts and techniques of spatial statistics. More recently, some studies have focused on understanding disease dispersal on a local and continental scale (ESKER et al., 2007; KIM et al., 2005; NUTTER et al., 2007). In fact, the importance of soybean rust onset to regional epidemics led to collaborative efforts to monitor disease occurrence in major soybean-producing regions in Brazil and the United States (EMBRAPA SOJA, 2007; USDA, 2007). These disease reports have been useful to the general public to assess regional disease status for timing fungicide sprays. Further analysis of the complete disease dataset should add valuable information on spatial and temporal dynamics of the disease in these regions.

Disease management. Current control of soybean rust primarily relies on fungicide applications. Compounds from triazole and strobilurin fungicide groups have been tested in

many locations and seasons exhibiting relatively high levels of disease control (MILES et al., 2007). Individual formulations of azoxystrobin, tebuconazole, difeconazole, and mixed formulations of epoxiconazole with pyraclostrobin reduced soybean rust severity on soybean plants inoculated from 4 days prior to 14 days after fungicide treatment (GODOY and CANTERI, 2004). For fast developing diseases such as soybean rust, chemical control efficiency also depends on correct timing of spraying. In the first two seasons after the discovery of soybean rust in Brazil, severe epidemics were observed in regions where fungicide applications were delayed as a consequence of slow disease diagnostics (YORINORI et al., 2005). Short fungicide supply, reduced availability of equipment for spray, and wet weather conditions may also contribute to delayed fungicide applications.

At locations with extremely favorable environmental conditions, vigorous monitoring is necessary for early detection of soybean rust at its onset and to anticipate chemical control. In Brazil, fungicide spray is recommended as a preventive measure or after early disease detection in the field (EMBRAPA, 2006). In some regions with extremely high epidemic pressure due to frequent rainfall, growers made five fungicide applications for disease control, but even so, yield losses were observed (SIQUERI, 2005).

Indirect yield losses due to soybean rust also include the costs for chemical control, particularly in regions where many applications are necessary. From 2001 to 2003, over a billion dollars was spent on chemical control of soybean rust in Brazil (De MORI and COSTAMILAN, 2004). In Tennessee, fungicide spray cost per hectare has been estimated from \$34 for one application to \$147 for three applications with 9.5% yield loss (GERLOFF et al., 2006). Additional yield losses up to 3% were estimated due to physical plant damage

from tractor tires during ground application (HOLSHOUSER and TAYLOR, 2006). According to this scenario, accurate disease risk assessments are fundamental to support decision making regarding the use of fungicide spray to avoid profit losses: no spraying could result in yield losses, while unnecessary spraying could increase production costs.

Few studies have been conducted on the effects of cultural control of soybean rust. Soybean rust is a polycyclic disease, and most of the epidemics develop from secondary infections. The occurrence of secondary infection cycles depends on environmental conditions. Cultural practices that reduce crop exposure to favorable growth conditions are likely to reduce disease development. In Brazil, an early planting date for early soybean maturity has been used to reduce the impact of soybean rust in regions where such practices are economically viable (YORINORI, 2007). Early-planted crops are exposed to reduced amounts of inoculum, which delay epidemic onset. Early harvesting of these varieties is anticipated; therefore, the period of crop exposure to environmental conditions favorable to soybean rust development is reduced. However, the effects of the planting date have been more significant in regions where no winter soybean is planted and early-season inoculum potential is low. In some major soybean-growing regions in Brazil, a quarantine period of 90 days with no soybean cropping during winter was imposed (YORINORI, 2007). In these regions, soybean rust onset was delayed for a month, and mild to moderate disease outbreaks were observed (EMBRAPA SOJA, 2007).

The effects of soybean plant population density on soybean rust have been studied, but the influence of row spacing on disease development is still unclear. No significant differences in disease development were observed at soybean row spacing of 18, 36, and 76

cm (ESKER et al., 2007). Soybean tends to compensate for small plant densities by growing laterally (HEIFFIG, 2002). At row spacing from 0.2 to 0.5 m and planting densities from 70,000 to 350,000 plants per hectare, soybean reached a high proportion of three-leaf area per ground area and lower canopy leaves were shaded after flowering (HEIFFIG, 2002). Adequate crop nutrition has improved plant development, which may increase the host's ability to tolerate pathogen development (FIXEN et al., 2007). Balanced fertilization with phosphorus (P) and potassium (K) has been associated with a reduction in soybean rust development (PPI, 1999). Application of NPK formulations at 30kg/ha reduced soybean rust severity and increased soybean yields (PICCIO and FRANJE, 1980).

Four resistance genes to soybean rust have been found in soybean. These gene are Rpp1 (MCLEAN AND BYTH, 1981), Rpp2 (BROMFIELD et al., 1980), Rpp3 (BROMFIELD and HARTWIG, 1980; BROMFIELD et al., 1980; HARTWIG and BROMFIELD, 1983), and Rpp4 (HARTWIG, 1986). However, different races of *P. pachyrhizi* have overcome the resistance of these genes (HARTMAN et al., 2005). So far, no complete resistance has been found for soybean rust on soybean varieties in the United States, but further screening is under way for lines exhibiting partial resistance (HARTMAN et al., 2005). In addition to soybean, other hosts such as common beans and perennial *Glycine* species are being investigated as potential sources for disease resistance (MILES et al., 2007; PATZOLDT et al., 2007; HARTMAN et al., 1992; HARTMAN et al., 2005).

Research trends

In the past decade, the expansion of soybean rust epidemics from Asia to western soybean-producing countries resulted in increased research efforts to expand the current

knowledge on soybean rust and to improve disease management. Rarely has one particular disease caused so much interest. Disease tracking systems have been established in Brazil, Argentina, and the United States to alert producers to disease outbreaks in major soybean regions (USDA, 2007; EMBRAPA SOJA, 2007; and FRIGIDI, 2005). Overwintering regions are monitored for pathogen survival and availability of early-season inoculum (WRIGHT et al., 2006; JURICK et al., 2007, EMBRAPA SOJA, 2007). In the United States, airborne spore concentration is monitored in many soybean-producing states during the growing season (KRUPA, 2006; BARNES and SZABO, 2007, RUPE and WIGLESWORTH, 2005). Also, computer simulations based on wind trajectories generate likely routes for spore dispersal (PAN et al., 2005; XUE et al., 2006; KIM et al., 2005). In addition, research and extension have worked together to teach growers to identify and manage the disease.

However, despite the recent advances in our understanding of soybean rust, disease outbreaks resulting in yield loss continues. The pathogen is endemic and severe epidemics are observed every year in regions with extremely favorable weather conditions, whereas unexpected severe outbreaks also occur occasionally at other locations. The risk for yield loss is considered high once the disease is observed at any location. This assumption prompts preventive disease control resulting in additional soybean production costs.

In some countries, studies have been made to assess the risk of disease outbreaks based on historical environmental conditions; however, the system was not applicable to assess the disease risk in real time (PIVONIA and YANG, 2004, 2005; REIS et al., 2004; MOSCHINI et al., 2005). Parameterization using experimental estimates of specific factors

triggering disease onset and affecting disease development would improve model simulation leading to better risk assessment for soybean rust outbreaks.

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CHAPTER 2: EFFECTS OF SHADE INTENSITY AND DURATION ON ASIAN SOYBEAN RUST

A.P.S. Dias¹, P.F. Harmon², C.L. Harmon², and X.B. Yang¹

¹ Iowa State University, 351 Bessey Hall, Ames, IA, 50011

² University of Florida, IFAS Plant Pathology, Gainesville, FL, 32611

Corresponding author: A.P.S. Dias, anapdias@iastate.edu

Abstract

Field studies were carried in Florida to quantify the effects of shade intensity and duration on Asian soybean rust (ASR) incidence and severity in the summer of 2006, fall of 2006, and summer of 2007. Potted soybean plants (Mycogen 5N351RR, maturity group 3.5) at V4 growth stage were inoculated with uredinospores of *Phakopsora pachyrhizi* in the evening (9 pm, 12 am, and 2 am) and placed in cages covered with shade cloth of different mesh sizes allowing light transmission rates (T) of 100%, 70%, 50%, or 20% of natural sunlight. Inoculated leaves from plants kept under shade (T = 20%) and no shade (T = 100%) were sampled 12, 18, and 36 hours after inoculation to determine rates of germination and formation of infection structures. After 12 days, the plants were rated for ASR incidence and severity. In another experiment, inoculated plants were placed in the shade (T = 20%) and removed to unshaded conditions (T = 100%) after 1, 2, and 7 days following inoculation. For control treatments, inoculated plants were also maintained in the shaded and unshaded

conditions for the duration of the experiment. All treatments were evaluated after 12 days for ASR incidence and severity. Our results suggest that plants receiving partial shade ($T = 70\%$, 50% , and 20%) had greater ASR incidence and severity compared to those under full sunlight ($T = 100\%$). Shade duration of more than 2 days increased both disease incidence and severity. Although shading did not affect either germination of uredinospores or the formation of appressoria and penetration pegs, the fact that shaded plants had greater disease severity suggests that postpenetration stages of ASR infection may be influenced by the degree of exposure to sunlight. Thresholds of inhibitory solar radiation intensity estimated in this study could be used to improve accuracy of risk predictions for ASR outbreaks.

Keywords: *Phakopsora pachyrhizi*, epidemiology, solar radiation, risk assessment

Introduction

Asian soybean rust (ASR), caused by *Phakopsora pachyrhizi*, is a major fungal disease in most soybean-producing regions worldwide. Fungal infection leads to premature defoliation of infected plants, especially in warm, humid environments (YANG et al., 1990). In some cases, defoliation has started at severity rates as low as 20% (YANG et al., 1990). Yield losses have been reported in plants with at least 20% premature defoliation at reproductive growth stages (YANG et al., 1990; VAKILI, 1979; BLESSITT et al., 2007).

Experimental results and field observations have suggested that *P. pachyrhizi* is sensitive to light (ISARD et al., 2006; KEOGH, 1974; KOCH and HOPPE, 1987; MARCHETTI et al., 1975; MELCHING et al., 1988; BROMFIELD et al., 1980). Germination was reduced when uredinospores are exposed to natural light (ISARD et al.,

2006; KEOGH, 1974). Negative phototropism of germ tubes was observed in controlled germination studies under artificial light (KOCH and HOPPE, 1987). The fungus may avoid direct sunlight exposure by producing uredinospores more abundantly on the abaxial compared to the adaxial side of leaves in the lower canopy (MARCHETTI et al., 1975; MELCHING et al., 1979; BROMFIELD et al., 1980).

Asian soybean rust is usually detected during the soybean reproductive stages, although younger plants are equally susceptible to the pathogen (MELCHING et al., 1988). After flowering, soybean leaves in a 0.38 m row-spaced canopy intercepted over 80% of the incident solar radiation (SAUER et al., 2007). On a regional scale, disease outbreaks coincided with reductions in solar radiation intensity due to cloudiness or late-season solar declination at tropical and temperate latitudes. In Brazil, Asian soybean rust was usually more severe after extended periods of rainy weather (Del PONTE et al., 2006). Also, severe ASR outbreaks are more frequently observed in regions of South Africa with prolonged cloudy periods during the summer (Eve du Preez, Pannar Seeds, KZN, South Africa, personal communication). During the summer months in Brazil, incident solar radiation is usually reduced by rain clouds and high moisture content in the atmosphere (CEBALLOS, 2005).

ASR usually expanded to temperate latitudes in Argentina, China, and the United States late in the fall when solar radiation intensity was reduced (FORMENTO and GIECO, 2007; YANG, 2005; USDA, 2007). In 2006, the majority of Asian soybean rust detections in the north-central United States occurred in October (USDA, 2007), when mean solar radiation intensity was reduced to half of the levels observed in the summer (PINKER,

2006). Quantifying relationships between sunlight availability and ASR establishment on soybeans could improve the accuracy of ASR risk assessments in major soybean-growing regions.

The objective of this study was to quantify the effects of shade intensity and duration on ASR incidence and severity.

Materials and methods

Phakopsora pachyrhizi was isolated from infected kudzu (*Pueraria montana* var. *lobata*) collected in Brandon, FL (Hillsborough County, 27.94°N–82.26°W) and maintained on soybean plants (Mycogen 5N351RR, maturity group 3.5). The planting density was four plants per 20-cm-diameter plastic pot. Infected plants were maintained in a greenhouse at the University of Florida (UFL, Gainesville, FL) and received irrigation and nutrients as needed.

Field experiments were conducted on a mowed bahiagrass (*Paspalum notatum*) field at UFL from June of 2006 to July 2007. For the shade intensity experiments, six trials were carried out during the summer and fall of 2006 and the summer of 2007 (Table 1).

Soybean plants (Mycogen 5N351RR, maturity group 3.5) were also sowed at a density of four plants per 10-cm-diameter clay pot. The plants were maintained in a greenhouse isolated from sources of ASR uredinospores for one month until trial days. Plants were watered and fertilized as needed to reach V3–V4 growth stages at the beginning of each trial. Similar plants were used in shade intensity, shade duration, and leaf germination experiments.

Shade intensity experiments. Inoculations were performed at 9 pm, 12 am, and 2 am (Table 1). Prior to each inoculation time, uredinospores were collected from ASR uredinia on attached leaves of greenhouse-grown plants with a vacuum pump connected to a cyclone separator. This equipment pumped air through a chamber and deposited dry uredinospores by impact on the bottom of a 15-ml plastic vial. The uredinospores were suspended in 50 ml of distilled sterilized water (DSW) containing one drop of Tween 20 for wet inoculation. Spore suspensions (0.1 ml) were incubated overnight at 25°C on 2.5-cm-diameter water-agar (1.5%) plates for assessment of spore germination ratios. The next morning, plates were stained with aniline blue lactophenol (2 g of soluble aniline blue suspended on 10 mL lactophenol). The first 100 uredinospores observed in the microscope field were examined at 100× to determine the proportion of germinated uredinospores. We assumed the spores were germinated when their germ tubes had grown twice the length of the uredinospores.

Eight soybean leaflets per pot received a single drop of 0.025 ml or 0.1 ml spore suspension in the 2006 and 2007 trials, respectively. Initial spore concentration was estimated using a hemacytometer (Hausser Levy Bright-Line, Hausser Scientific, Horsham, PA), and the concentration of final spore suspension was adjusted according to the inoculation volume so that each leaflet was inoculated with 5×10^3 uredinospores.

After inoculation, sets of three or four clay pots were placed either uncovered or in wooden frames (1.2 m × 1.2 m × 0.7 m) covered with shade cloth allowing the transmission (T) of different levels of sunlight for shading treatments: full sunlight (T = 100%) and partial sunlight (T = 70%, T = 50%, and T = 20%) (Figure 1). In the 2007 trials, uninoculated pots of soybeans were placed in the field as negative controls. The experimental units, sets of

inoculated soybean pots that had received the combination of inoculation time and light transmission levels, were rated 12 days after inoculation for ASR incidence (ratio of infected leaves) and severity rate of leaves exhibiting the following: 0) no lesions; 1) 1–2 lesions; 2) 3–10 lesions; 3) 11–30 lesions; and 4) >30 lesions. No soybean rust lesions were observed in the negative controls.

In 2006, the experimental units were arranged in a split-plot block design with two replicates, whereas in 2007, a completely random design with four replicates was used. Disease incidence data were analyzed in SAS (SAS Institute, Cary, NC) by the MIXED procedure (method type 3) for the 2006 trials and by the GLM procedure for the 2007 trials to estimate least square means and determine least significant treatment differences at $P = 0.05$. Disease severity data were analyzed nonparametrically in SAS by the LD-CI macro and the combination of RANK and MIXED procedures to estimate relative treatment effects and confidence intervals at $P = 0.05$ based on a ranking of severity rates (SHAH and MADDEN, 2004).

Shade duration experiments. Two trials were carried out in the fall of 2006 and in the summer of 2007. Sets of three or four soybean pots were inoculated at 9 pm as described previously and placed either in an open field uncovered or in shade cloth-covered cages allowing the transmission (T) of full sunlight ($T = 100\%$) and shade ($T = 20\%$). Shaded pots were moved to the open field ($T = 100\%$) after 1, 2, or 12 days in the 2006 trial and after 1, 2, 7, or 12 days in the 2007 trial. The shade duration (SD) treatments, arranged in a completely random design, were applied to two replicates in the 2006 trial and to four replicates in the 2007 trial. The sets of inoculated soybean plants receiving different shade duration

treatments constituted the experimental units. Twelve days after inoculation, the plants were rated for ASR incidence (percentage of symptomatic leaves) and severity as done for the shade intensity experiments. The incidence and severity data were analyzed in SAS as described previously.

Weather assessment. On the day following inoculation, soybean leaf temperatures ($^{\circ}\text{C}$) and global solar irradiation (W m^{-2}) were recorded under the different light transmission treatments. Leaf temperatures were recorded every 3 hours with a handheld infrared thermometer (Raytek ST60 XB, Raytek Co., Santa Cruz, CA). The presence of leaf wetness was visually assessed every hour after sunrise following inoculation by checking the absorption of water by Kimwipes (Kimtech Science, Kent, UK) lightly wiped on randomly sampled soybean leaves from shaded and unshaded treatments. Average incident solar irradiation was recorded at 5-minute intervals with a data-logger radiometer (Radiometer PMA2100, Solar Light Co., Glenside, PA) connected to a sensor (PMA2140) for incoming global solar irradiation within a 400 to 1100 nm wavelength range. The integrated daily solar radiation ($\text{MJ m}^{-2} \text{d}^{-1}$) was compared to the estimated incidence (%) standardized by the largest values in each trial.

Spore germination on leaf surface. Four sets of two soybean pots were inoculated at 9 pm as described previously and placed either in an open field ($T = 100\%$) or in shade cloth-covered cages ($T = 20\%$) arranged in a completely random design. Aliquots (0.1ml) of uredinospore suspensions (5×10^4 uredinospores/ml) were incubated overnight on 2.5-cm-diameter plates containing water-agar (1.5%) for assessment of uredinospore germination. Five leaflets were sampled from each set of pots 12, 18, and 36 hours after inoculation.

Following each sampling time, samples (2 cm²) excised from the center of each leaflet were placed on 100 mL of glacial acetic acid and 95% ethanol (1:1) for clearing at 45°C. After 2 hours, cleared leaf segments were washed twice in distilled water, stained with aniline blue lactophenol for 10 minutes, washed twice in distilled water to remove excess stain, and observed under a compound microscope at 400×. Subsamples of 100 germinated uredinospores were examined to determine the percentage exhibiting the following: 1) germ tubes, 2) germ tubes with immature appressoria, 3) germ tubes with mature appressoria, and 4) germ tubes with appressoria and penetration pegs. Pots of inoculated soybean plants were kept in shade treatments for 12 days until the evaluation for ASR incidence and severity. Data on leaf germination, disease incidence, and disease severity were analyzed in SAS as described previously.

Results

In general, neither inoculation times nor interactions of inoculation times and shade intensity levels significantly affected ASR incidence and severity (data not presented). Light intensity levels significantly affected both ASR incidence and severity (data not presented). Increasing sunlight transmitted through a shade cloth reduced ASR incidence and severity on inoculated soybean leaves (Tables 2 and 3). Soybean rust incidence was always greater in the partial sunlight treatments, especially under 20% and 50% light transmission, than in full sunlight (Table 2). However, exposure to full sunlight did not completely prevent *P. pachyrhizi* from infecting soybean leaves (Table 2). The infected leaves observed in shade treatments had greater disease severity rates compared to those observed in full sunlight (Table 3). Large relative treatment effects observed in shaded treatments suggest that shaded

infected leaves tended to exhibit larger severity rates compared to the combination of infected leaves from shaded and unshaded treatments (Table 3). Our results on disease incidence and severity suggest that inoculated plants in the shade tended to exhibit larger number of symptomatic leaves and those leaves had larger numbers of lesions compared to unshaded inoculated plants.

Increasing shade duration resulted in greater ASR incidence and severity (Table 4). In the 2007 trial, overall disease incidence was lower than in 2006, and ASR was detected only in treatments shaded for at least 2 days (Table 4). In both trials, disease severity rates were similar in inoculated treatments receiving from 0 to 2 days of shading (Table 4).

In general, disease was reduced at daily solar radiation levels greater than $10 \text{ MJ m}^{-2} \text{ day}^{-1}$ (Figure 2). Although this trend was observed in all trials, the reduction in ASR incidence was more pronounced in the summer trials at solar radiation greater than $10 \text{ MJ m}^{-2} \text{ day}^{-1}$ (Figure 2).

Leaf temperatures were similar for leaves exposed to different shade intensities, although slightly higher temperatures were observed in the fall of 2006 compared to the summer of 2006 and 2007 (data not presented). The highest leaf temperatures were usually recorded in unshaded treatments at noon, but the differences were within the equipment's range of error (Figure 3). The duration of leaf wetness was usually similar for shade intensity treatments, with shaded treatments usually exhibiting an additional half-hour leaf wetness compared to unshaded treatments. The surface of inoculated leaves in shaded and unshaded treatments was usually completely dry by 10 am on the day following inoculation.

No significant differences in spore germination were observed on leaf surfaces placed in the open field ($T = 100\%$) or in shade ($T = 20\%$). Average germination rates of 80% were observed both on agar and on leaf surfaces 12 hours after inoculation. Half of the germinated uredinospores produced appressoria by morning (12 hours after inoculation), but no increases in germination rates or appressoria and penetration peg formation were found under open-field or shade treatments during the following 24 hours (Table 5). However, the consistent reduction in ASR severity on soybeans exposed to full sunlight in the open field compared to that on the shaded soybeans suggest that light may have inhibited later stages of the infection process (Figure 4).

Discussion

Our results suggest that Asian soybean rust is more prevalent and severe under low-light conditions. This is in agreement with field observations and other studies of Asian soybean rust epidemics. In commercial fields, the disease is usually first detected on soybean leaves in the lower canopy after flowering. At the reproductive stage, the soybean leaf area index often reaches four units in 0.38m row-spaced cropping systems, and only 20% of the incident solar radiation is likely to reach lower canopy leaves (SAUER et al., 2007). Lesions and uredinia develop more frequently and uredinospores are more exposed on abaxial leaf surfaces compared to the upper surface, thereby escaping direct sunlight exposure (MARCHETTI et al., 1975; MELCHING et al., 1979; BROMFIELD et al., 1980).

Besides shade, other weather conditions that are favorable to disease development, such as stable temperatures, high air moisture content, and prolonged leaf wetness, often affect the lower canopy. However, we designed our experiments to minimize variation of

these variables among the shade treatments. Average air and leaf temperatures were usually within the range reported to be favorable for infection, and night temperatures were within the optimal range for germination (KOCHMAN, 1979; MELCHING et al., 1989; MARCHETTI et al., 1976). All treatments had the minimum period of leaf wetness required for spore germination (MARCHETTI et al., 1975). Therefore, we found no evidence that variation of weather conditions, other than solar radiation intensity, confounded the effects of shading on Asian soybean rust incidence and severity.

The fact that shading for more than one day following inoculation was necessary for disease development suggests that solar radiation may affect postgermination processes in ASR infection. However, we found no evidence of light inhibition on appressoria and penetration peg formation in this study. In germination studies of some rusts, including Asian soybean rust, uredinospore germination was reportedly reduced by light (KEOGH, 1974; ISARD et al., 2006; JOSEPH and HERING, 1997). ASR uredinospores did not germinate after exposure to more than 25 MJ m^{-2} of solar radiation distributed over 2 days (ISARD et al., 2006). Germination of *Uromyces viciae-fabae* was delayed until evening on sunny days, but occurred earlier under the canopy on cloudy days (JOSEPH and HERING, 1997). Reduced germ tube elongation of *P. pachyrhizi* was observed on light-exposed uredinospores, and germ tubes exhibited negative phototropism, which was enhanced by blue light (KEOGH, 1974; KOCH and HOPE, 1987). To avoid reductions in spore germination and germ tube elongation in our studies, plants were inoculated in the evening. Uredinospore germination usually started after 2 hours in the dark; germination rates over 50% were observed after 6 hours. Similar observations were reported in previous studies (MAGNANI

et al., 2007; KOCHMAN, 1979). In the morning following inoculation, most uredinospores were germinated on leaf surfaces with developing appressoria and penetration pegs. Normally, soybean rust appressoria are initially observed 6 hours after inoculation, and penetration pegs are formed within the following 12 hours (MCLEAN and BYTH, 1981; KOCH et al., 1983; YANG, 1991). The production of prepenetration structures was similar on both shaded and unshaded soybeans. However, disease severity rates were still lower on unshaded soybean plants compared to shaded ones after 12 days. Similarly, there were reports of increasing numbers of lesions on soybeans kept in the dark for up to 16 hours following inoculation, although penetration rates remained constant after 8 hours of darkness (BONDE et al., 1976).

Some soybean defense mechanisms are elicited by light, which might explain possible effects of sunlight on ASR colonization (WARD and BUZZELL, 1983; GRAHAM and GRAHAM, 1991; STOSSEL, 1982). Similar ASR colony growth and haustoria formation have been observed on susceptible and resistant soybean cultivars up to 24 hours after inoculation when plants were kept in the dark (MCLEAN, 1979). However, only susceptible cultivars had increased fungal growth and haustoria formation when the plants were exposed to light (MCLEAN, 1979; KEOGH et al., 1980). The delay in colony growth on resistant cultivars was associated with increasing numbers of necrotic host cells near the infection site. This reaction was attributed to the activation of host defense mechanisms such as accumulation of the phytoalexin glyceollin in the resistant cultivar (KEOGH et al., 1980; MCLEAN, 1979; De MORTEL, 2007). Furthermore, many studies have reported that the production of glyceollin and precursors on soybeans is dependent on light (WARD and

BUZZELL, 1983; GRAHAM and GRAHAM, 1991; STOSSEL, 1982). Soybean seedlings incubated for more than 12 hours under light had 30 times higher glyceollin concentration and exhibited greater resistance to *Phytophthora megasperma* f.sp. *glycinea* than seedlings incubated in the dark (WARD and BUZZELL, 1983). Our observations and experimental results consistently suggest that Asian soybean rust is more severe under shade conditions, which might be explained by the effects of sunlight on the interactions between the pathogen and host.

We observed reduced disease incidence at solar radiation intensities greater than 10 MJ m⁻² day⁻¹. Similar solar radiation levels are often observed in the fall at temperate latitudes or on cloudy days in the tropics (CEBALLOS, 2005; PINKER, 2006). After the summer solstice that occurs in June and December, respectively, for northern and southern hemispheres, the days get progressively shorter and incident radiation is reduced by the solar declination. This effect is particularly noticeable towards the autumn in temperate latitudes (IQBAL, 1983). In the summer of 2006, average solar radiation intensity of 15 MJ m⁻² day⁻¹ was observed in the central United States (PINKER, 2006). Radiation levels dropped to 8 MJ m⁻² day⁻¹ in the fall, coinciding with the time that Asian soybean rust outbreaks expanded northward (USDA, 2007). On a regional scale, rain clouds and atmospheric humidity similarly contribute to reduce solar radiation by absorbing or reflecting incident radiation (DOGNIAUX, 1994; WELCH et al., 1980). Average solar radiation intensities under 12 MJ m⁻² day⁻¹ are usually accumulated during cloudy days in soybean-producing regions in Brazil (CEBALLOS, 2005). This range is comparable to the radiation intensities favoring greater Asia soybean rust incidence observed in this study. Indeed, soybean rust outbreaks were

reportedly most severe in regions with frequent rainfall distributed over many rainy and cloudy days (SIQUERI, 2005; Del PONTE et al., 2006).

Disease assessment models based on comprehensive relationships between climate and disease epidemics are useful to anticipate risks of disease outbreaks (PIVONIA and YANG, 2005). Such information is valuable to guide decision making for adequate disease prevention and control. Further analyses of the influence of cloudiness on the temporal and spatial development of Asian soybean rust are under way, based on the results from this study.

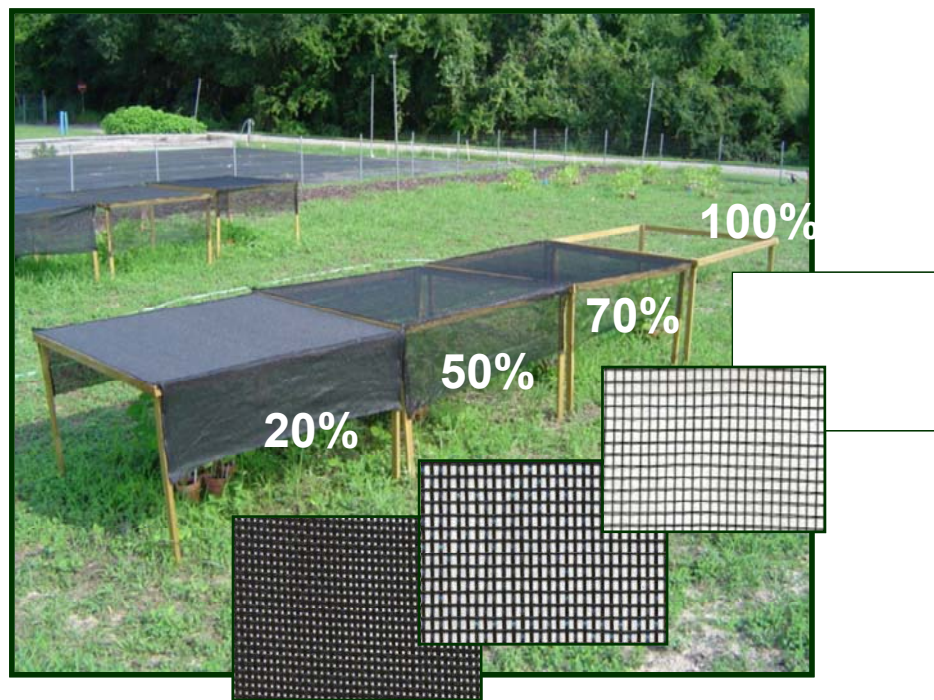
Figures and Tables

Figure 1: Cages covered with shade cloth allowing different transmission levels of solar radiation. Observed sunlight transmission rates were 100%, 70%, 50%, and 20% of incident solar global radiation.

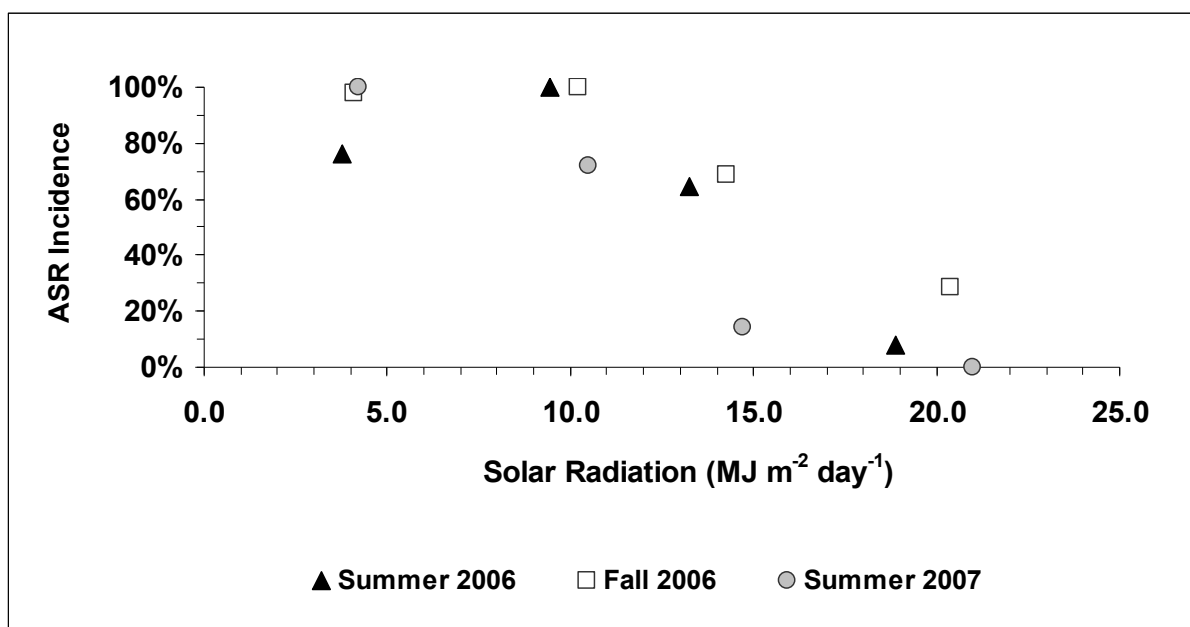


Figure 2: Asian soybean rust (ASR) incidence at different daily solar radiation intensities (MJ m⁻² day⁻¹) in three trials. Trials were carried out during the summer and fall of 2006 and the summer of 2007. Incidence values were standardized to the highest values observed in each trial.

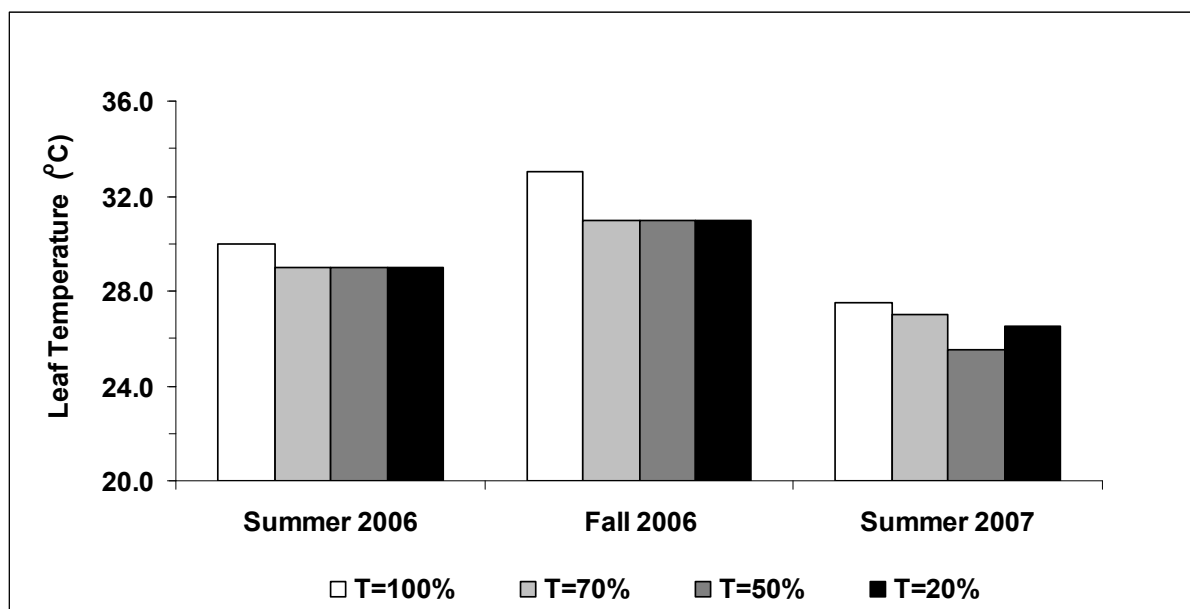


Figure 3: Soybean leaf temperatures ($^{\circ}\text{C}$) recorded at noon in cages covered with shade cloth allowing solar radiation transmission rates of 100%, 70%, 50%, and 20% in three trials. Trials were carried out during the summer and fall of 2006 and the summer of 2007. A maximum error range of 1°C is reported by the manufacturer of the infrared thermometer used in these measurements (Raytek Co., Santa Cruz, CA).

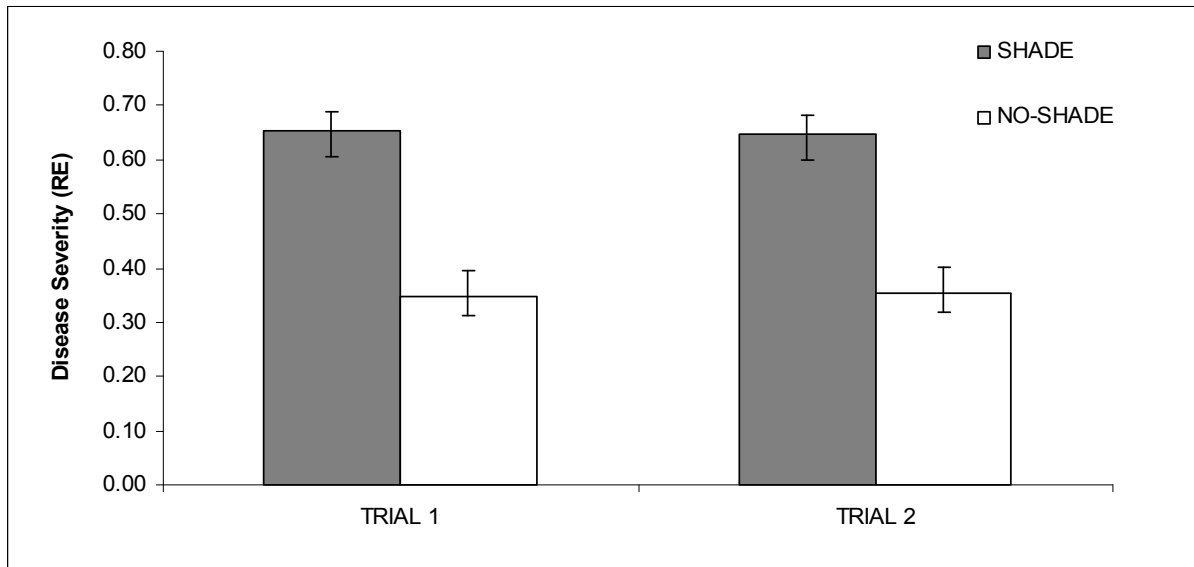


Figure 4: Relative effects (RE) of shade treatments on Asian soybean rust severity rates 12 days after inoculation in two trials with four replicates. Inoculated soybean plants were maintained in shaded and unshaded environments for spore germination and preinfection studies; leaves were evaluated for disease severity after 12 days. Treatments with larger estimates of relative treatment effects tend to exhibit greater severity rates compared to the combination of all treatments. Error bars represent the confidence intervals of the mean RE at $P = 0.05$.

Table 1: Description of treatments and average environmental conditions recorded the day after inoculation in six trials

Trials ¹	Inoculation Date	Inoculation Time ²	Sunlight Transmission (%)	I _{RAD} (MJ m ⁻² d ⁻¹)	Leaf Wetness (hr)	T _a (°C)	T _n (°C)
1. Summer/2006	28/06/2006	2am	20/50/70/100	19.0	8.0	27.5	-
2. Summer/2006	10/07/2006	9pm/12am	20/50/70/100	-	7.5	27.0	23.0
3. Fall/2006	31/08/2006	12am/2am	20/50/70/100	14.5	9.5	27.5	25.5
4. Fall/2006	01/09/2006	9pm	20/50/70/100	20.5	10.0	28.5	25.0
5 Summer/2007	06/06/2007	9pm	20/50/70/100	21.0	6.0	27.5	24.0
6. Summer/2007	17/06/2006	9pm/2am	20/100	25.5	6.0	28.5	24.0

^{1.} Environmental variables were monitored in unshaded conditions and included incident solar radiation (I_{RAD}, MJ m⁻² day⁻¹), number of hours of leaf wetness, average air temperature (T_a, °C), and night air temperature (T_n, °C).

^{2.} Different soybean plants were inoculated at different times during the night, and placed under shade to receive different proportions of natural sunlight.

Table 2: Mean incidence (%) of Asian soybean rust estimated on inoculated soybean plants receiving different proportion of natural sunlight (%) in three experiments

Trial	Proportion of Sunlight (%)	Incidence (%)
Summer 2006	20	34.7
	50	45.5
	30	29.3
	100	3.5
	LSD ¹	5.7
Fall 2006	20	96.5
	50	97.9
	30	85.4
	100	58.3
	LSD	8.0
Summer 2007	20	95.0
	100	58.3
	LSD	7.9

¹. LDS represents significant differences for treatments in the same experiment at P = 0.05.

Table 3: Asian soybean rust severity estimates on plants in unshaded (light transmission T = 100%) and shaded (T = 20%) environments for 12 days in two trials

Year	Treatment	Median Severity Rate ¹	Rank	RE ²
2006	Shade	4	18.0	0.73 (0.69–0.77)
	No Shade	3	7.0	0.27 (0.23–0.31)
2007	Shade	3	8.5	0.67 (0.51–0.73)
	No Shade	2	4.5	0.33 (0.27–0.48)

¹ Estimates include median severity rate, mean rank of severity rates, and relative treatment effects with respective confidence intervals at P = 0.05.

² Relative treatment effects (RE) were calculated nonparametrically based on the ranking of treatment severity rates (SHAH and MADDEN, 2004). Treatments with larger estimates of relative treatment effects tend to exhibit greater severity rates compared to the combination of all treatments.

Table 4: Asian soybean rust mean incidence, median severity rate, and mean rank of severity rates

Trial Year	Days in the Shade	Incidence (%)	Median Severity Rate	Mean Rank	RE ^{1, 2}
2006	0	26.9	2	3.5	0.38 (0.375–0.385)
	1	55.9	2	3.5	0.38 (0.375–0.385)
	2	64.2	2	3.5	0.38 (0.375–0.385)
	12	91.7	4	7.5	0.88 (0.875–0.885)
	LSD	16.1			
2007	0	0.0	0	6.5	0.30 (0.240–0.380)
	1	0.0	0	6.5	0.30 (0.240–0.380)
	2	3.1	0	9.9	0.47 (0.240–0.720)
	7	13.3	1.5	13.9	0.67 (0.410–0.820)
	12	10.9	2	15.8	0.76 (0.580–0.850)
	LSD	9.2			

¹. Relative treatment effects (RE) with respective confidence intervals (P = 0.05) estimated in inoculated soybean plants maintained in the shade to receive 20% of natural sunlight for 0, 1, 2, 7, and 12 days until the evaluation in two trials. LSD represents least significant differences of incidence for treatments in the same trial at P = 0.05.

². Relative treatment effects were calculated nonparametrically based on the ranking of treatment severity rates (SHAH and MADDEN, 2004). Treatments with larger estimates of relative treatment effects tend to exhibit greater severity rates compared to the combination of all treatments.

Table 5: Total number of germinated Asian soybean rust uredinospores exhibiting germ tubes only (GT), germ tubes with appressorium (AP), appressoria with penetration pegs (PP), germ tubes with a swelling appressorium (SAP), and plant cell discoloration under appressoria (DISC) 12, 18, and 36 hours after inoculation on plants kept under unshaded and shaded (20% of natural radiation) conditions in two trials

Treatment	Hours	Germinated	GT	AP	PP	SAP	DISC
No Shade	12	606	112	494	125	203	0
		(25) ¹	(48)	(28)	(12)	(36)	(0)
	18	350	49	258	92	17	2
		(14)	(4)	(13)	(4)	(6)	(1)
	36	433	41	389	-	70	180
		(38)	(27)	(52)		(4)	(42)
Shade	12	649	79	518	117	174	0
		(4)	(25)	(25)	(1)	(28)	(0)
	18	353	42	289	86	22	0
		(25)	(14)	(11)	(6)	(10)	(0)
	36	466	106	348	-	129	41
		(35)	(66)	(45)	-	(23)	(27)

¹ Values in parentheses are the standard deviation of the observations in four replicates.

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CHAPTER 3: MODELING THE EFFECTS OF CLOUDY WEATHER ON REGIONAL EPIDEMICS OF ASIAN SOYBEAN RUST

A.P.S.Dias¹, C. V. Godoy², X. Li¹, and X.B.Yang¹

¹ Iowa State University, 351 Bessey Hall, Ames, IA, 50011

² Embrapa Soja, CP 231, Londrina, PR, Brazil, 86001-970

Corresponding author: A.P.S. DIAS, anapdias@iastate.edu

Abstract

Several studies in controlled environments suggest that Asian soybean rust (ASR) epidemics are enhanced by shaded conditions similar to those observed on cloudy days. ASR epidemics in Brazil were correlated to the number of rainy days, which were usually characterized by continuous cloud cover. These observations suggest that adding shade effects of clouds to disease models may improve prediction of ASR epidemics. The present study simulated daily ASR development based on cloud cover conditions, using experimentally derived estimates of reduction in apparent infection rates in unshaded conditions. Our estimations were validated on a regional scale with field reports of seasonal epidemic intensities and disease progress curves in Brazil and South Africa. To determine ASR incidence in shaded and unshaded environments, experimental studies were carried out at the University of Florida, Gainesville, FL. Disease incidence in shaded and unshaded

conditions was analyzed to determine the relationship between shading and apparent infection rates. The experimental estimates were applied to simulate ASR on a regional scale using a semi-empirical logistic model parameterized according to the observed cloud cover conditions. Depending on weather data availability, cloudy days were assumed to be either i) days with less than 2 hours of full sun or ii) days with complete cloud cover in all three daily observations done in the morning, afternoon, and evening. Estimated disease progress curves and final estimates of epidemic intensity were compared to field reports in 30 growing seasons in 11 regions of Brazil and South Africa. Severe ASR epidemics occurred when 19.5 cloudy days were reported during the period from first disease detection to the date of disease assessment at the end of the growing season in Brazil and South Africa. Mild epidemics were observed in years with less than eight cloudy days. Our estimates were consistent with the observed ASR severity using the correlation coefficient $r = 0.96$ and a linear regression slope close to 1.

Keywords: *Phakopsora pachyrhizi*, epidemiology, solar radiation, and risk assessment

Introduction

Asian soybean rust (ASR), caused by *Phakopsora pachyrhizi*, has been reported in most soybean-growing regions worldwide. In Brazil, ASR was first observed during the 2001–02 season, and outbreaks have been observed in many regions (YORINORI et al., 2005). Severe epidemics have also been reported frequently in the mist belt zone of KwaZulu-Natal province (E. DUPREEZ, personal communication). Although seasonal disease epidemics in tropical regions have required preventive management with fungicide sprays, yield losses were still observed in regions with favorable weather conditions (LEVY, 2005; YORINORI, 2007).

Experimental results and field observations have suggested that *P. pachyrhizi* is sensitive to light (KEOGH, 1974; KOCH and HOPPE, 1987; MARCHETTI et al., 1975; MELCHING et al., 1979; BROMFIELD et al., 1980). Germination is inhibited by sunlight and germ tubes grow in the opposite direction from a light source (KEOGH, 1974; KOCH and HOPPE, 1987). Sporulation is usually more abundant on the abaxial side of lower canopy leaves, where exposure to direct sunlight is minimal (MARCHETTI et al., 1975; MELCHING et al., 1979; BROMFIELD et al., 1980). In controlled field experiments, ASR incidence and severity were greater in the shade than in full sun (DIAS, 2007).

In the tropics, severe epidemics of ASR are often observed in regions where prolonged rainfall periods occur (Del PONTE et al., 2006). In addition to providing favorable humidity and temperature conditions, rainfall may also favor Asian soybean rust epidemics by providing the shading that promotes pathogen development and infection. Similarly,

reduced sunlight intensity is also observed at midlatitudes in the fall when the intensity and duration of sunlight are naturally reduced by solar declination. In the fall ASR epidemics usually expand to temperate latitudes in Argentina, China, and United States (FORMENTO and GIECO, 2007; YANG, 2005; USDA, 2007).

Modeling approaches have employed weather variables to assess potential inoculum survival and epidemic development of ASR (PIVONIA and YANG, 2004; PIVONIA and YANG, 2005; Del PONTE et al., 2006; YANG et al., 1991; REIS et al., 2004; MOSCHINI et al., 2005; KIM et al., 2005). These studies used weather factors as predictors to assess disease development. However, few studies have addressed the effects of shading on soybean rust development, and sunlight has never been used as a model input.

We hypothesized that the apparent infection rate of ASR is influenced by solar radiation intensity. The objectives of this study were: i) to estimate the reduction in ASR apparent infection rates in unshaded environments; ii) to develop a simulation model to estimate seasonal disease progress from apparent infection rates regulated by cloud cover conditions; and iii) to validate our simulations with regional reports of seasonal epidemics in Brazil and South Africa.

Materials and methods

Data collection and preliminary analysis. ASR development was simulated in eight regions of Brazil and three regions in South Africa during different growing seasons totaling 30 distinct rust epidemics (Figures 1 and 2; Table 1). Climate data were provided by the national weather service in each country: Instituto Nacional de Meteorologia (INMET,

Brazil) and the South African Weather Service (SAWS, South Africa). Weather stations within 100 km of each growing region were selected to provide climate data.

Daily observations of rainfall, relative humidity, cloudiness, and temperature were summarized over the main soybean growing season in each region, which usually extends from November to March. Although most weather data were collected similarly in both countries, cloudiness was estimated using different procedures. In Brazil, the number of hours of direct sunlight per day was recorded. In this study, days were arbitrarily assumed to be cloudy when less than 2 hours of direct sunlight was observed. In South Africa, the fraction of the sky covered by clouds was recorded every day by a trained observer at 00, 12 and 18 hours coordinated universal time (UTC). In this study, days were considered cloudy when the sky was more than 7/8 covered by clouds during all three observations.

Seasonal weather variables were compared, including total precipitation (Pp), number of rain days (Nrd), number of cloud days (Ncd), average maximum and mean temperatures (Tx and Tm), and the proportion of days with high relative humidity allowing dew formation (Pdd). The PROC CORR procedure was used to estimate significant Pearson's correlation in SAS at $P = 0.05$ (SAS Institute, Cary, NC). The number of cloudy days required for different epidemic intensities was estimated in SAS using the PROC GLM procedure (SAS Institute, Cary, NC).

Regional epidemics of Asian soybean rust can be classified empirically as light, moderate, and severe based on average severity rating, yield losses, mean defoliation, and number of fungicide sprays (Table 2). Plant pathologists in Brazil and South Africa estimated the intensity of ASR epidemics at the end of the main growing season based on one or more

of these criteria (Table 1). For specific locations in Brazil, seasonal ASR progress curves were also available (MARTINS et al., 2004, 2005, 2006; ROSSETO and OLSON, 2004; IAMAUTI et al., 2004a and b; TOFOLI and OLSON, 2004; WRUCK et al., 2004).

Parameter estimation. Field trials were carried out on mowed turfgrass at the University of Florida in 2006 and 2007 to test the effects of shading on Asian soybean rust establishment (DIAS, 2007). Inoculated potted soybean plants (Mycogen 5N351RR, maturity group 3.5) were placed for 12 days in either shade (provided by shade cloth with 20% solar radiation transmission) or in full sunlight (100% solar radiation transmission) until evaluation for incidence of ASR. Disease incidence rates were normalized to the largest values in each trial and treatment means were estimated and statistically compared at $P = 0.05$.

To estimate apparent infection rates under different light conditions, ASR development in shade and full-sunlight conditions was assumed to follow the monomolecular model with all plants initially healthy ($Y_{M0} = 0$) and maximum possible disease intensity equal to 1 at time n (Eq. 1).

$$Y_{Mn} = 1 - (1 - Y_{M0}) * \exp(-r_M * t) \quad \text{Eq. 1}$$

Y_{Mn} = disease incidence after time $t = n$

Y_{M0} = disease incidence at time $t = 0$

r_M = monomolecular apparent infection rate

The monomolecular model is appropriate when disease develops exclusively from primary inoculum (MADDEN et al., 2007). In our trials, there was no time for secondary infections to develop since disease assessment was made 12 days after inoculation.

Therefore, the observed variability in ASR incidence basically relied on different apparent infection rates in the shade compared to full sunlight.

Under the assumptions of zero initial incidence and uniform primary inoculum, we calculated the rate of change (α) in the apparent infection rates (r_M) in full-sunlight compared to shade conditions. The estimation was based on average final disease incidence observed in both environments within the time period of 12 days (Eq. 2–4).

$$Y_{M < SHADE >} = 1 - \exp(-r_M * t) \quad \text{Eq. 2}$$

$$Y_{M < SUNLIGHT >} = 1 - \exp(-\alpha * r_M * t) \quad \text{Eq. 3}$$

$$\alpha = \frac{\ln(1 - Y_{M < SHADE >})}{\ln(1 - Y_{M < SUNLIGHT >})} \quad \text{Eq. 4}$$

Model development and validation. The development of ASR in natural conditions most likely follows the logistic pattern with maximum disease intensity at 1 (Eq. 5). The logistic model has been used to represent the epidemics of polycyclic diseases such as ASR (VANDERPLANK, 1963; MADDEN et al., 2007). In this model, increments in disease intensity are regulated by a constant logistic apparent infection rate (r_{Ln}) multiplied by the proportions of both diseased (Y_{Ln}) and healthy plants ($1 - Y_{Ln}$) at time $t = n$. The development of a polycyclic disease relies on secondary inoculum produced on the diseased plants during epidemics. In this sense, increasing proportions of diseased plants (Y_{Ln}) producing secondary inoculum would result in increasing daily increments of diseased plants while the proportion of healthy plants would be greater than the proportion of diseased plants.

The logistic apparent infection rate (r_{Ln}) represents infection efficiency and production of secondary inoculum (MADDEN et al., 2007; TENG, 1985). Environmental and host characteristics negatively affecting infection and sporulation reduce the apparent infection rate (r_{Ln}) (MADDEN et al., 2007, JEGGER, 2004; TENG, 1985). In this study, we assumed that the logistic model explained disease development, but the apparent infection rate (r_{Ln}) was adjusted daily as a function of cloudiness on any given day. The maximum apparent infection rate (r_{Ln}) of ASR was set to occur on cloudy days. The maximum infection rate was reduced by a fraction α on clear days as calculated from our experimental data.

$$dY/dt = r_{Ln} * Y_{Ln} * (1 - Y_{Ln}) \quad \text{Eq. 5}$$

Unlike monomolecular models, logistic models increase from an established initial disease level. In this study, most of the simulations were set to start at the first detection date reported in the region at a severity level of 1 lesion per leaf (0.4–0.8%). This is the minimum detectable level for a trained observer previously reported for ASR (GODOY et al., 2006). One exception was made for the 2002–2003 growing season in Brazil, when ASR was observed for the first time in many regions. At that time, disease observers were not yet trained to either identify the disease in early stages or to prevent epidemic development. Therefore, the first detection dates did not reflect minimum detectable levels since the disease was just noticed when premature defoliation began to affect yield (YORINORI and LAZZAROTTO, 2004). Epidemics of ASR were considered to have started at least a month earlier in those regions (YORINORI and LAZZAROTTO, 2004). For this growing season in Brazil, disease simulations started one month before the reported detection dates. In South Africa, the detection dates of ASR were not regularly reported. The simulations were

arbitrarily set to start on December 1st because most of soybean fields are usually already planted at that time and inoculum is locally present (CALDWELL and LAING, 2002).

Starting on the detection dates, daily increments of disease severity were calculated from the current ratios of healthy to diseased plant tissue multiplied by the adjusted apparent infection rate. This rate was selected every day according to the daily cloudiness condition as either r_{LM} or $\alpha * r_{LM}$, for cloudy and unclouded days. Daily disease increments were integrated for estimation of disease progress curves and final epidemic intensity at harvest time (Table 2). Final disease estimates were compared to the reported intensity of epidemics observed in each location and season (Table 1). Estimated disease progress curves were compared to disease progress curves of untreated plots in fungicide trials at specific locations (MARTINS et al., 2004, 2005, 2006; ROSSETO and OLSON, 2004; IAMAUTI et al., 2004a and b; TOFOLI and OLSON, 2004; WRUCK et al., 2004).

Results

The number of cloudy days had a significant positive correlation with total precipitation and number of rainy days (Table 3). A negative correlation was observed between cloudy days and average mean temperatures, and the correlations between cloudy days and maximum temperature and proportion of dew days were nonsignificant at $P = 0.05$ (Table 3).

Severity of ASR was strongly correlated to the number of cloudy days (Table 3). Severe ASR epidemics were reported in regions with more than 19.5 cloudy days observed between the first disease detection and the disease assessment date (Table 4). Disease

epidemics were much less severe with minimum yield losses in regions with less than 8 cloudy days (Table 4).

Overall, the cloudiness-based model accurately predicted regional development of Asian soybean rust resulting in light, moderate, and severe epidemics. Ninety-four percent of the epidemics had final intensity accurately estimated from cloud cover conditions over disease development. However, the model overpredicted the intensity of two in 30 epidemic cases. In this study, no final epidemic intensity was underestimated.

In general, predicted and observed disease progress curves of seven disease epidemics were similar, resulting in moderate and severe final disease intensity (Figures 3 and 4). The joint correlation between predicted and observed disease severity was estimated to be 0.976 with a regression line slope of 1.02 (Fig. 4). The residuals were randomly distributed over time of epidemic development and also over observed disease severity (Figure 5). Nonetheless, the model had a tendency to slightly overpredict disease severity at low disease severity levels.

Discussion

Cloud cover was a good estimator of apparent Asian soybean rust infection rates, resulting in accurate predictions of the disease's temporal progress and final epidemic intensity. Clouds provide daytime shading, which seems to be favorable for soybean rust development. Field observations and experimental results support the positive effects of shading on Asian soybean rust development (KEOGH, 1974; KOCH and HOPPE, 1987; MARCHETTI et al., 1975; MELCHING et al., 1979 and BROMFIELD et al., 1980; DIAS,

2007). In the field, the disease has been detected most frequently on shaded canopy leaves with lesions mostly formed on lower leaf surfaces that receive little direct sunlight (MARCHETTI et al., 1975; MELCHING et al., 1979 and BROMFIELD et al., 1980). Results of controlled experiments suggested that ASR incidence and severity are higher on shaded soybean (DIAS, 2007). High disease incidence was only observed on soybeans exposed to levels of solar radiation comparable to those recorded on cloudy days in the tropics (DIAS, 2007).

Besides shading, cloud cover may also have incorporated other biologically important weather factors to explain regional ASR development. *P. pachyrhizi* requires specific ranges of leaf wetness in terms of time and temperature for infection and development (MARCHETTI et al., 1976). In tropical regions, summer rain events provide moisture and prolonged shading by rain clouds reducing average temperatures. At most locations in our study, the numbers of cloudy and rainy days were positively correlated, while the number of cloudy days and average air temperature were negatively correlated.

From a modeling stand point, cloud cover was an appropriate estimator variable on a regional scale because it exhibited large spatial correlation within regions. Rainfall, temperature, and leaf wetness have been employed alone or in combination to estimate ASR severity (YANG et al., 1991; REIS et al., 2004; KIM et al., 2005; Del PONTE et al., 2006). However, although data collection of these weather variables is straightforward, large variations are observed within relatively close locations; therefore, more observations are required to characterize these variables on a regional scales. In tropical regions of Brazil, similar cloud cover is observed over hundreds of kilometers (TIBA, 2000). In this case, few

observations are necessary to determine regional cloud cover conditions, which simplifies data input of the cloud cover–based simulation model on a regional scale. In many locations of Brazil and South Africa, cloud cover is regularly observed and weather data are usually available to the public by the national weather service (INMET and SAWS).

In just two of 30 epidemic cases, our model slightly overpredicted final disease intensity compared to the field reports. Both cases were first-time disease outbreaks, so evaluator inexperience may have influenced research ratings of actual disease severity (GODOY et al., 2006, YORINORI and LAZZAROTTO, 2004). Nonetheless, our cloudiness-based model was robust over subjective variations in disease rating since most predictions of ASR severity were consistent with observations from different disease evaluators.

Our cloud cover–based model was successfully extrapolated over time and space. The model structure permitted simulations to be initiated at different times and crop stages over a number of regions. However, the model had a strong assumption on disease severity levels at first detection time. Model estimates were based on daily epidemic buildup from initial disease levels. Starting severity values should reflect actual disease values at the starting time so that disease increments are accumulated over accurate initial levels.

Regional risk for severe ASR outbreaks can be estimated in our simulation model from historical patterns of cloud cover. Backwards model simulations would determine critical timing for disease onset leading to yield losses based on regional cloud cover patterns during soybean reproductive stages. In general, later ASR onset in a region results in shorter time for disease development. Accurate simulation results would give support for decision making of appropriate management strategies to avoid profit losses on a regional scale.

Figures and tables

Figure 1: States of Brazil. Circles represent soybean-producing regions included in the simulations with the cloud cover-based model: MT (Mato Grosso); GO (Goiás); BA (Bahia); MG (Minas Gerais); SP (São Paulo); MS (Mato Grosso do Sul); and RS (Rio Grande do Sul).

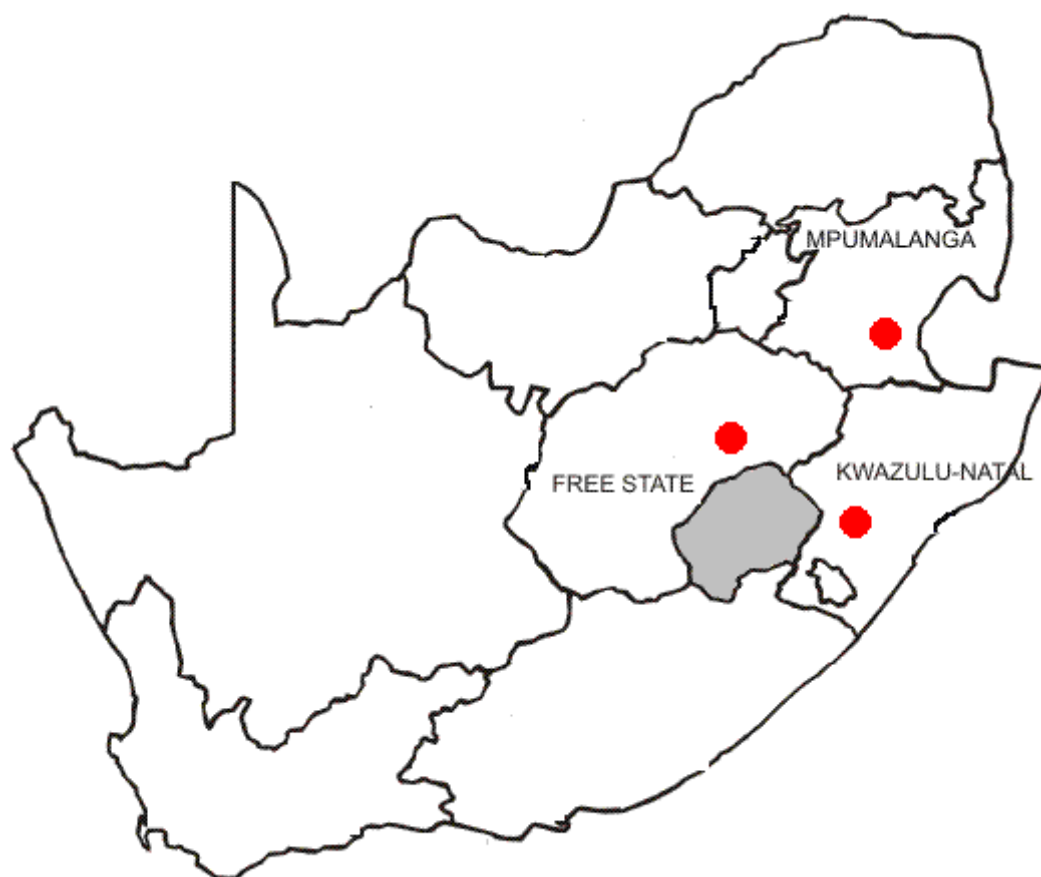
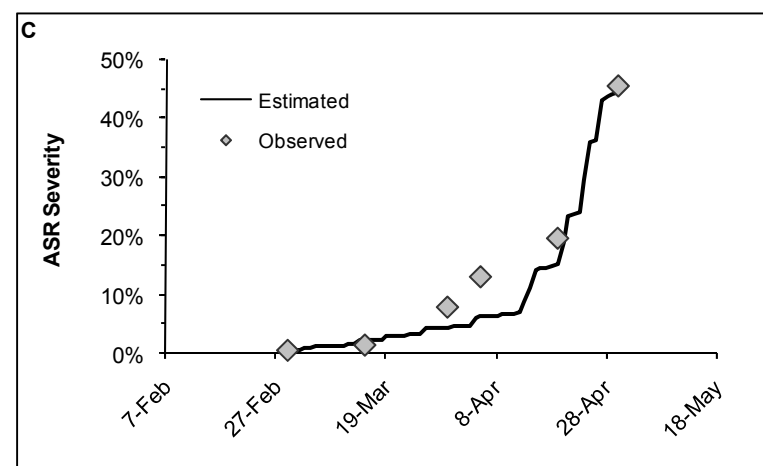
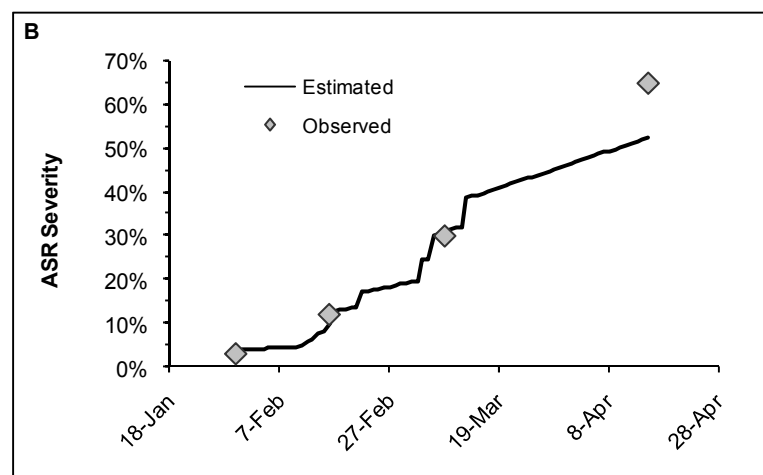
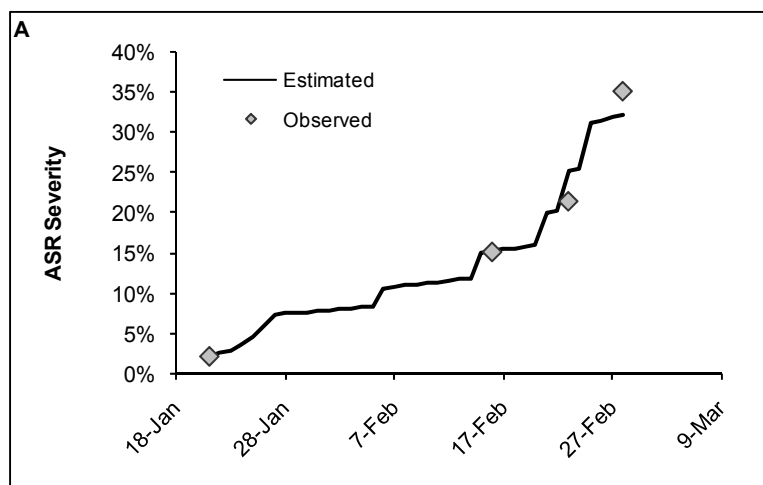


Figure 2: Provinces of South Africa. Circles represent soybean-producing regions included in the simulations with the cloud cover-based model.



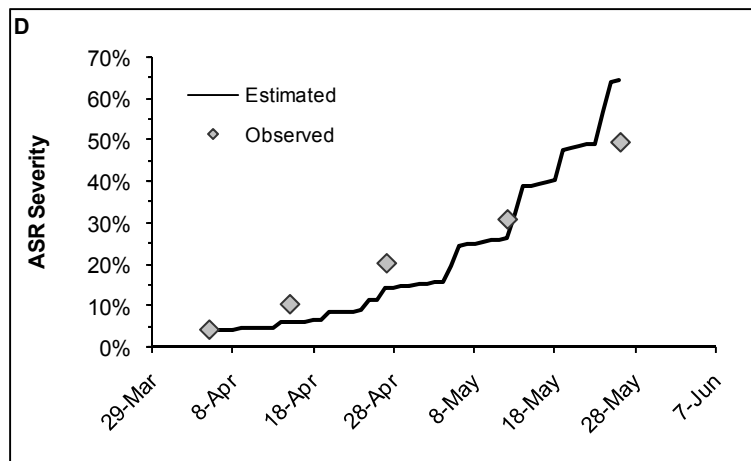


Figure 3: Estimated Asian soybean rust progress curves using the cloud cover-based model and observed disease severities at four location in Brazil: A) Uberaba, MG, 2003 (WRUCK et al., 2004); B) Barreiras, BA, 2004 (MARTINS et al., 2005) ; C) Mogi Mirim, SP, 2003 (IAMAUTI et al., 2004a and b); and D) Itaberá, SP, 2003 (ROSSETO and OLSON, 2004).

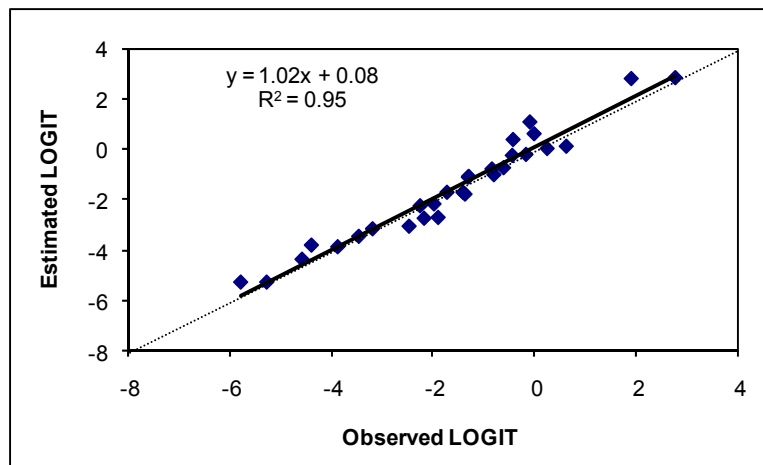


Figure 4: Estimated versus observed Asian soybean rust severity linearized to LOGITS during the epidemic progress at seven locations in Brazil. The solid line represents the solution for the regression equation and the dotted line represents values of correlation equal to one.

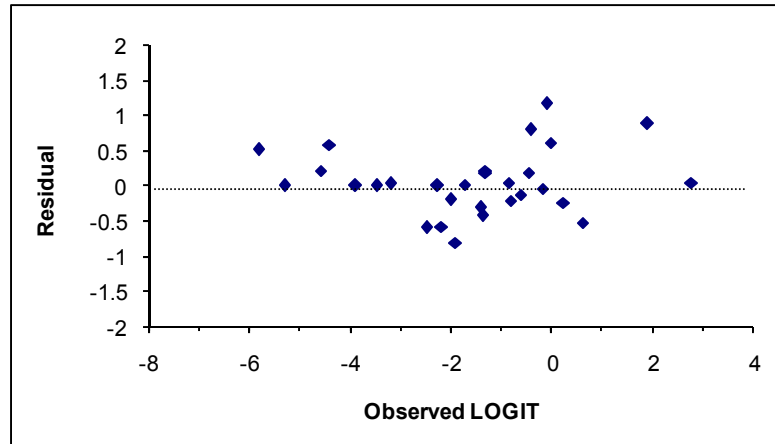


Figure 5: Residual plot of estimated ASR severity during the epidemic progress at seven locations in Brazil.

Table 1: Soybean growing regions and seasons with the reported first detection dates and final epidemic intensity in Brazil and South Africa

Region	Growing Season	Detection Dates ¹	Epidemic Intensity	Disease Data Source
BRAZIL				
Southeastern	2004-05	16-Dec-04	Severe	SIQUERI, 2005
Mato Grosso	2005-06	11-Dec-05	Severe	SIQUERI, 2005
	2006-07	6-Dec-06	Moderate	EMBRAPA SOJA, 2007
Central Mato Grosso	2004-05	30-Dec-04	Light	SIQUERI, 2005
	2005-06	28-Dec-05	Light	SIQUERI, 2005
Western	2002-03	7-Feb-03	Severe	OLIVEIRA, 2005
Bahia	2003-04	15-Jan-04	Light	OLIVEIRA, 2005
	2005-06	16-Jan-06	Light	GODOY et al., 2006
	2006-07	22-Dec-06	Moderate	EMBRAPA SOJA, 2007
Northern	2004-05	14-Feb-05	Light	BALLARDIN et al., 2005
Rio Grande do Sul	2005-06	12-Jan-07	Light	BALLARDIN et al., 2005
	2006-07	11-Jan-07	Light	EMBRAPA SOJA, 2007
Southeastern	2002-03	15-Dec-02	Severe	NUNES JR. et al., 2005
Goiás	2003-04	09-Dec-03	Severe	NUNES JR. et al., 2005

	2005-06	30-Dec-06	Moderate	GODOY et al., 2006
	2006-07	27-Dec-06	Severe	EMBRAPA SOJA, 2007
Northwest São Paulo	2002-03	31-Jan-03	Light	AZEVEDO, 2005
	2003-04	18-Dec-03	Severe	AZEVEDO, 2005
	2004-05	12-Jan-05	Light	AZEVEDO, 2005
Triangle	2003-04	09-Dec-04	Severe	JULIATTI, 2005
Minas Gerais	2004-05	15-Dec-04	Moderate	JULIATTI, 2005
Mato Grosso do Sul	2004-05	28-Dec-04	Light	ANDRADE, 2005
	2005-06	30-Nov-05	Severe	GODOY et al., 2006
SOUTH AFRICA				
Mist Belt	2003-04	-	Severe	DUPREEZ, 2006
KwaZulu-Natal	2004-05	-	Severe	DUPREEZ, 2006
	2005-06	-	Severe	DUPREEZ, 2006
Mpumalanga	2003-04	-	Light	DUPREEZ, 2006
Province	2004-05	-	Moderate	DUPREEZ, 2006
	2005-06	-	Severe	DUPREEZ, 2006
Free State	2005-06	-	Light	DUPREEZ, 2006

¹. First detection dates were reported by Embrapa, Brazil (www.cnpso.embrapa.br/alerta/).

Table 2: Mean severity rates (%), estimated yield losses (%), mean defoliation (%), and average number of required fungicide sprays at different epidemic intensity levels

Epidemic Intensity	Mean Severity	Yield Losses	Defoliation	Number of Fungicide Sprays
Light	<20%	0 - 15%	<10%	0 to 1
Moderate	20 - 40%	15 - 30 %	10 - 30 %	1 to 2
Severe	>40%	30 - 70%	30 - 60%	≥2

Sources: YANG et al., 1990; HARTMAN et al., 1991; De MORI and COSTAMILAN, 2004.

Table 3: Estimates of Pearson's correlation among weather variables and disease severity observed at 30 epidemic locations from disease detection to disease assessment date in Brazil and South Africa

	Ncd	Nrd	Pp	Tx	Tm	Pdd
Ncd	-	-	-	-	-	-
Nrd	0.560*	-	-	-	-	-
Pp	0.396*	0.604**	-	-	-	-
Tx	-0.353	-0.616**	-0.596**	-	-	-
Tm	-0.487*	-0.567*	-0.572**	0.735	-	-
Pdd	0.090	0.664*	0.532	-0.378	-0.278	-
SEVERITY	0.786**	0.413*	0.195	-0.104	-0.313	-0.022

Ncd: number of cloudy days; Nrd: number of rainy days; Pp: precipitation (mm); Tx: average maximum temperature (°C); Tm: average mean temperature (°C); Pdd: proportion of days with dew formation.

* Values followed by (*) are significant at $P = 0.05$.

** Values followed by (**) are significant at $P = 0.01$.

Table 4: Expected number of cloudy days and standard errors estimated from 30 epidemic locations in Brazil and South Africa.

LSM		
Epidemic Intensity	Cloudy Days	SE
Light	7.9 a ¹	1.35
Moderate	13.6 b	1.91
Severe	19.5 c	1.23

¹Estimates followed by different letters differ at P = 0.05.

Light: disease severity <20%; Moderate: disease severity = 21–39%; Severe: disease severity >40%.

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CHAPTER 4: REGIONAL DEVELOPMENT OF ASIAN SOYBEAN RUST RELATED TO SOLAR RADIATION PATTERNS IN BRAZIL AND THE UNITED STATES

A.P.S.Dias, X. Li, and X.B.Yang

Iowa State University, 351 Bessey Hall, Ames, IA, 50011

Corresponding author: A.P.S. DIAS, anapdias@iastate.edu

Abstract

Spatial and temporal patterns of Asian soybean rust (ASR) occurrence were examined from data collected during four years in north-central Brazil and in two years in the central United States. Initial disease detections during a growing season were assumed to be those closest to major inoculum sources. Euclidian distances from locations of initial detections to locations of subsequent detections were computed and analyzed. Datasets of estimated incoming solar irradiance in three growing seasons were analyzed to estimate the mean solar radiation intensity at locations of disease detection. Simple regression analysis was used to estimate spatial and temporal patterns of disease front movement in each season. Pearson's correlation and multiple regression analysis were calculated to estimate the significance of solar radiation intensity as a covariate on time of disease frontal movement. In general, the movement of Asian soybean rust in Brazil and the United States followed a non-wavelike pattern with an exponential distribution. Frontal movement rates varied among months and

growing seasons. Distance from initial detections and solar radiation intensity at vegetative and reproductive soybean stages had significant positive time correlations to disease detection. Our results suggest that Asian soybean rust tends to appear with a high level of solar radiation intensity. To our knowledge, this is the first comparison of spatial epidemiology of ASR in two countries, and the first study to identify possible impacts of the spatiotemporal spread on ASR epidemics.

Keywords: *Phakopsora pachyrhizi*, epidemiology, solar radiation, and risk assessment

Introduction

As we have shown, Asian soybean rust (ASR), caused by *Phakopsora pachyrhizi*, is considered the most threatening disease in major soybean-producing regions worldwide (YORINORI et al., 2005; JOHANSSON et al., 2006; IVANCOVICH, 2005; LEVY, 2005; KRISHNA and NAIK, 2001). In Brazil, early-season disease onset usually resulted in severe defoliation and yield losses when environmental conditions were favorable for epidemic development (SIQUERI, 2005). Although the disease has not caused severe damage in major soybean regions of the central United States, collaborative efforts have been made to educate farmers and extension workers and to track disease movement (USDA, 2007). ASR tracking systems were established in Brazil and the United States to monitor disease onset at major soybean regions (USDA, 2007; EMBRAPA SOJA, 2007).

Few studies have addressed the spatial epidemiology of Asian soybean rust. Most of the research has been on regional distribution of the disease over large countries such as China and Australia (TSCHANZ and SHANMUGASUNDARAM, 1984; STOVOLD and SMITH, 1991). However, concepts and techniques of spatial statistics were rarely applied. More recently, some studies have focused on understanding disease dispersal on a local and continental scale (ESKER et al., 2007; KIM et al., 2005; NUTTER et al., 2007). A linearized expansion rate was estimated to be 18 km/day in the 2006 epidemics in the central United States (CHRISTIANO and SCHERM, 2007). ASR was assumed to arrive in the north-central United States during mid- to late season in comparison to other rusts and based on prevailing temperature characteristics at particular locations (PIVONIA and YANG, 2005).

The quantification of ASR movement patterns from inoculum source regions may add valuable information on disease dynamics during the season, thereby improving risk assessment models for disease outbreaks. In Brazil, the most important sources of ASR inoculum are located near central regions where soybean is cultivated year long (YORINORI, 2007). However, it is still uncertain whether the regions of winter cropping are indeed the only inoculum source to neighboring soybean regions. In the United States, ASR is likely to overwinter at latitudes below 30°N including coastal zones in Louisiana and Texas (PIVONIA and YANG, 2004). With continuously favorable conditions, the disease front would be expected to move from inoculum source regions in a wavelike pattern with constant frontal velocity (MADDEN et al., 2007). However, more realistically the disease front is likely to move from inoculum source regions at variable velocities since heterogeneous environmental conditions affect disease progress throughout the season resulting in non-wavelike epidemic expansion patterns (MADDEN et al., 2007).

Unfavorable weather conditions for ASR development include average air temperatures above 27°C, leaf wetness periods under 6 hours per day, and mean solar radiation intensity above 10 MJ m⁻² day⁻¹ (MARCHETTI et al., 1976; KEOGH, 1974; DIAS, 2007). ASR is sensitive to light, and direct sunlight exposure results in reduced germination and germ tube growth rates, negative phototropism of germ tubes, and reduced disease incidence and severity (KEOGH, 1974 and KOCH and HOPE, 1987, DIAS, 2007). Although disease onset is usually noticeable after soybean is at reproductive stages, older leaves are not necessarily more susceptibility compared to younger ones (DADKE et al., 1996;

MELCHING et al., 1988). In this case, additional characteristics of established soybean canopy such as lower leaf shading should favor disease development.

The objectives of this study were to: i) geo-reference and map ASR detection locations in Brazil and the United States; ii) calculate the monthly rates of ASR front movement in these countries; and iii) analyze solar radiation as a covariate to the spatial process of ASR movement.

Materials and methods

Disease detection data collection and processing. Dates of Asian soybean rust detection in different municipalities in Brazil were summarized from disease reports released during four growing seasons from 2003 to 2007 (EMBRAPA SOJA, 2007). For this study, when multiple detection dates in a municipality were observed in a growing season, the first reported date was assumed to be the detection date. Although ASR was observed in southern Brazil during the growing seasons in the study, only epidemics in the main soybean-growing states of north-central Brazil were analyzed (Figure 1). In the United States, counties and dates of ASR detection in a growing season were summarized from disease reports in 2006 and 2007 (USDA, 2007). Although ASR detections were reported in Florida and the eastern United States, only detections in the Mississippi Basin were analyzed for this study (Figure 2).

Disease detection locations were geo-referenced to central geographical coordinates of the municipalities (Brazil) and counties (U.S.) using the standard World Geodesic System of 1984 (WGS84, revised in 2004). Detection dates were converted to days in the growing

season, assuming the soybean growing season starts on Oct 1st in Brazil and May 1st in the United States.

The locations of first disease detections in a growing season were assumed as the closest to main spore sources where the pathogen overwinters. In central Brazil, *P. pachyrhizi* overwinters at irrigated sites where soybean is cultivated year long, but the contribution to inoculum survival by volunteer soybean and other wild hosts is still unclear. In the United States, the pathogen is likely to overwinter in southern Texas and coastal Louisiana (PIVONIA and YANG, 2004). Euclidean distances were calculated from sites of the first seasonal disease detections to subsequent detection locations during six growing seasons. The rate of disease front movement was analyzed assuming the disease was at similar detectable levels when first reported at each location.

Solar radiation data collection and processing. Estimations of incident solar irradiation (W m^{-2}) using a similar GOES-8 satellite imagery approach are available for Brazil (Pentad Matrix GL1.2 (V01), CPTEC/INPE) and the United States (Surface Radiation Budget Data, GCIP/GAPP). In independent studies from these companies, solar irradiance was calculated based on cloud cover characteristics and ground reflectance with an estimated error ranging from $0.5\text{--}1.0 \text{ MJ m}^{-2}\text{day}^{-1}$ (CEBALLOS and BOTTINO, 2006; CEBALLOS et al., 2004; PINKER, 2006). The average solar irradiance was computed for the central coordinates of square grids of 0.4° and 0.5° , respectively, in Brazil during 2003–04 and 2004–05 (CEBALLOS et al., 2004) and in the United States during 2006 (PINKER, 2006). For these studies, estimates of mean solar irradiance were integrated to daily solar radiation ($\text{MJ m}^{-2} \text{ day}^{-1}$) at each point using median monthly day length (IQBAL, 1980) during the

growing season months in Brazil (October to February) and the United States (June to October).

Point estimates of solar radiation were converted to surface maps using the radial basis function method with a completely regularized spline calculated from 8 to 12 neighboring points to minimize the mean square errors (ArcMap 9.2, ESRI, Redlands, CA). From the surface maps, estimates of mean solar radiation intensity were extrapolated to the locations where ASR was detected in the same growing season.

Statistical analysis. The relationship between disease detection timing and distance and solar radiation were explored using PROC CORR and PROC REG for estimation of Pearson's correlation and multiple regression analysis (SAS Institute, Cary, NC). The dependent variable was fixed as days in the growing season. The date for first disease detection at a given site was assumed to be a function of distance from sites of initial detections in a region and average solar radiation intensity in the months corresponding to soybean vegetative (R_{VG}), flowering (R_{FL}), and seed filling (R_{SF}) stages (November, December, and January in Brazil and June, July, and August in the United States). Best model fits were selected based on highest R^2 , smallest root mean square error (RMSE), and randomness of residual distribution. The model variables were checked for multi-collinearity based on their variance inflation factors (VIF).

Results

The farthest regions where Asian soybean rust was detected at the end of the soybean season had similar distances from source regions in all six epidemics analyzed in this study

(Figures 3 and 4). ASR was detected at 1000 and 1500 km, respectively, from the first detection sites in Brazil (Figure 3) and the United States (Figure 4). However, spatiotemporal movement of disease fronts occurred at different rates in each growing season (Figures 3 and 4). From 2003 to 2006 in Brazil, the disease expanded in a similar non-wavelike pattern following an exponential distribution (Figure 3). During the first month of epidemics, ASR was detected at average distances of 300 km from the initial detection sites (Figures 5). Subsequent disease expansion rates fluctuated from 50 to 400 km per month. In the 2006 growing season, ASR was reported only in November, a one-month delay in epidemic onset compared to previous years (Figure 5A and 5B).

Comparable exponential disease front movement was observed in the United States (Figure 4). In 2006, the disease was first observed in July, and foci stayed concentrated within an average distance range of 200 km for three months until September (Figure 5C). In October, the disease quickly reached distances up to 1200 km with average distance of 657 km from the initial detection sites. In June of 2007, Asian soybean rust was reported at mean distances of 500 km in the central United States (Figure 5C). From July to September, the disease front slowly moved northward to mean distances of 647 km. In October, expansion rate accelerated to distances up to 1500 km with final mean expansion of 715 km from the initial detection sites (Figure 4).

Solar radiation intensity was different in Brazil and in the United States during the studied soybean seasons (Figures 6–8). On average, monthly solar radiation intensity was consistent between the 2004 and 2005 growing seasons in Brazil, with the average intensity up to $12.1 \text{ MJ m}^{-2} \text{ day}^{-1}$ observed in February of 2005 (Table 1). The lowest solar radiation

intensity was usually observed in January, when soybeans are at the reproductive stage (Figure 1). During the 2006 growing season in the United States, solar radiation intensity gradually decreased from $14.8 \text{ MJ m}^{-2} \text{ day}^{-1}$ in June to $7.9 \text{ MJ m}^{-2} \text{ day}^{-1}$ in October (Table 1). In general, ASR detection occurred at locations receiving less than $12 \text{ MJ m}^{-2} \text{ day}^{-1}$ of solar radiation in both countries (Figures 6–8).

Solar radiation data was extrapolated to locations where ASR was detected during three growing seasons in Brazil and the United States. Time of disease detection was significantly correlated to distance from initial detection regions and solar radiation intensity at soybean vegetative and reproductive stages (Table 2). In multiple regressions, solar radiation intensity significantly contributed to estimation of time to disease onset in addition to the distance from initial detection sites (Table 3). The estimated parameters for the solar radiation variables were consistently positive, suggesting that ASR was observed later in the growing season at locations with higher solar radiation intensity levels (Table 3). Multi-collinearity was not observed within the tested variables resulting in variance inflation factor (VIF) values below 2 units (Table 3). On average, increments of $1 \text{ MJ m}^{-2} \text{ day}^{-1}$ of solar radiation at soybean's vegetative stages corresponded to a delay of 17 days to disease detection at similar distances.

Discussion

In this study, maps of Asian soybean rust reports in Brazil and the United States were produced for characterization of spatial and temporal patterns of disease epidemics. Collaborative efforts in the two countries have provided charts of ASR detection dates and locations (EMBRAPA SOJA, 2007; USDA, 2007), but datasets have been neither geo-

referenced nor visually explored. Preliminary analysis of spatial processes would usually begin with the production of meaningful maps and distance calculations.

ASR expanded exponentially in all six studied growing seasons, but monthly disease movement rates did not necessarily increase over time. Previous studies have suggested that constant frontal velocity is usually inappropriate to realistically describe disease spread (FERRANDINO, 1993; SCHERM, 1996; MINOGUE, 1989). In contrast, dispersive wave models with increasing frontal velocity have been proposed (SCHERM, 1996; MINOGUE, 1989).

By comparison to U.S. epidemics, we found no evidence that local inoculum sources anticipated disease onset at soybean regions farther than 500 km from major overwintering regions in central Brazil. The regions of pathogen overwintering are still undefined in Brazil, although winter temperatures do not usually restrict pathogen survival except for some regions in northeast Brazil (PIVONIA and YANG, 2004). In fact, ASR is only consistently reported during the winter in central regions where soybean is cultivated year long (EMBRAPA SOJA, 2007). In the United States, *P. pachyrhizi* is only likely to survive in southern states at latitudes below 30°N. Still, the disease front moved 500 km in the first three epidemic months in the United States, which resembled the patterns observed in Brazil.

Unlike most epidemics in this study, ASR stayed confined under 200 km distances from initial detection sites observed in July 2006. Asian soybean rust was predicted to appear in the soybean belt in late season, based on other rust patterns and specific temperature requirements for disease development (PIVONIA and YANG, 2005). The front rapidly

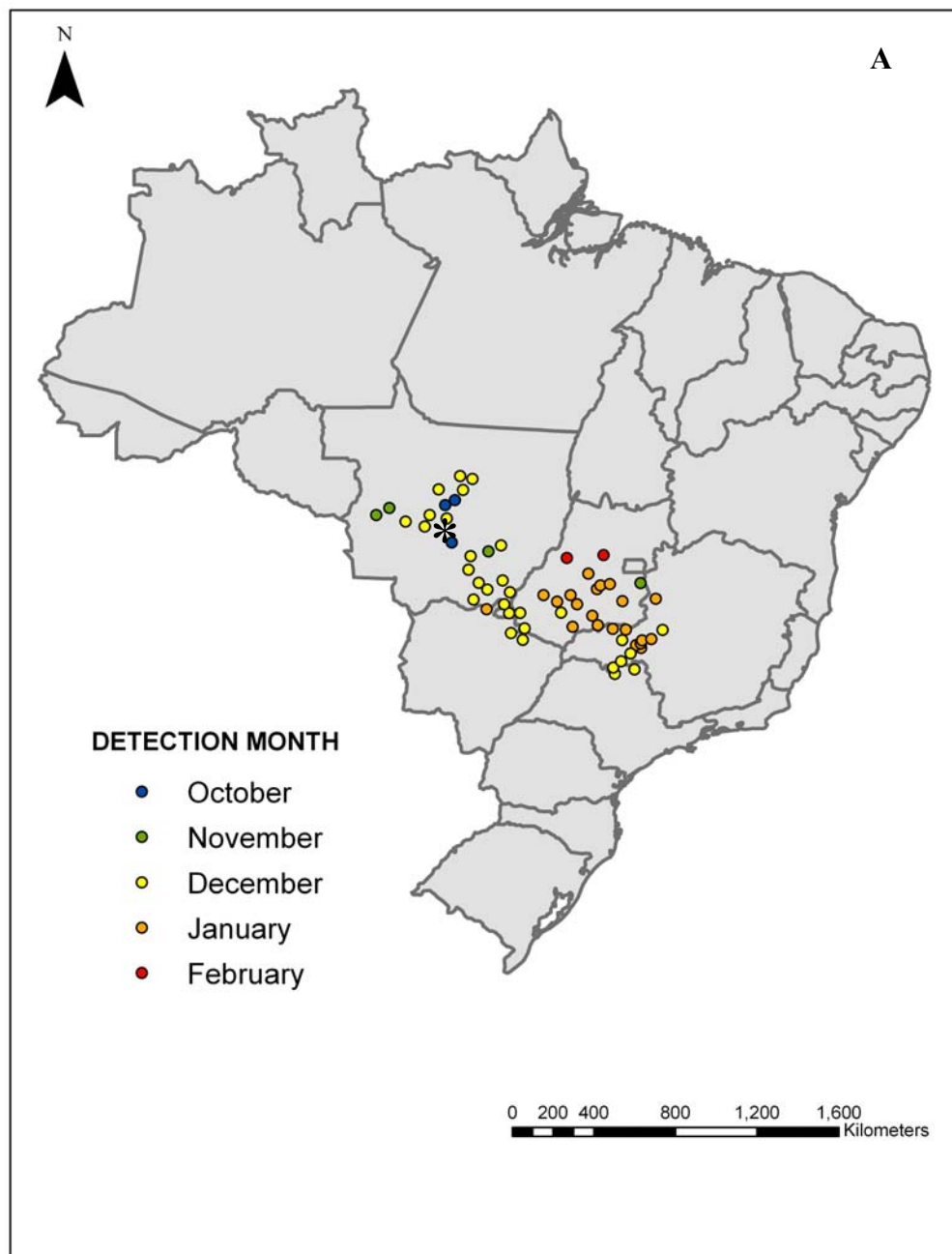
spread to reach average distances of 900 km in October, when soybean crops were at the harvesting stage (PEDERSEN, 2004).

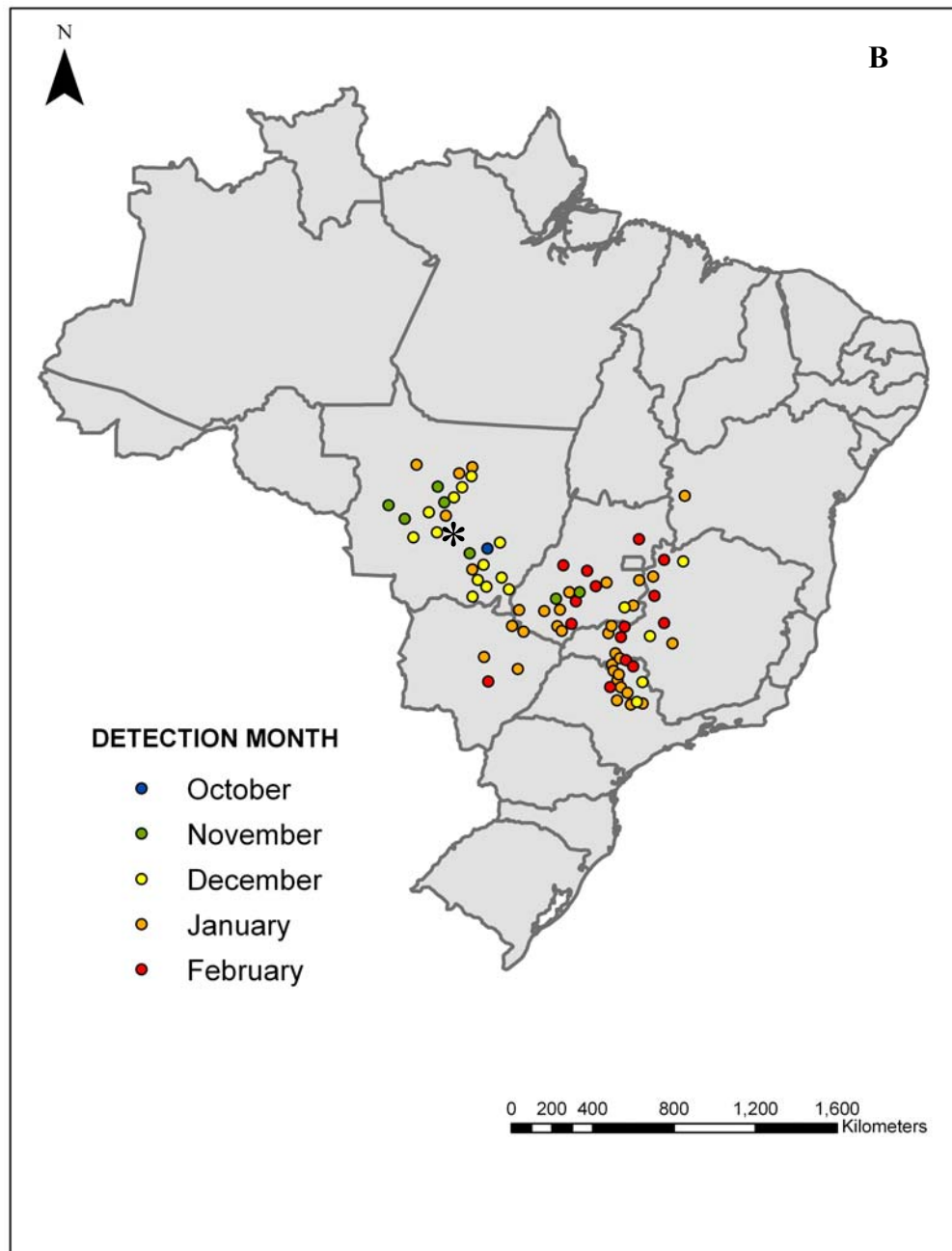
Significant positive correlations and model parameters between time to disease detection and solar radiation intensity were estimated at locations of disease detections. Our estimations are in agreement with previous observations that ASR is sensitive to sunlight. A period of shading is required for infection and fungal development since direct light inhibits spore germination, germ tube growth, and sporulation (KEOGH, 1974; KOCH and HOPPE, 1987; DIAS, 2007). ASR incidence and severity on soybean was gradually reduced as solar radiation intensity increased above $10 \text{ MJ m}^{-2} \text{ day}^{-1}$ (DIAS, 2007). Severe ASR epidemics occurred after at least 16 cloudy days in Brazil and in South Africa (DIAS, 2007). Despite solar radiation, a number of environmental factors also influence Asian soybean rust establishment (MARCHETTI et al., 1976; Del PONTE et al., 2006; KEOGH, 1974; KOCH and HOPPE, 1987; DIAS, 2007). Infection is inhibited at temperature less than 27°C , especially in leaf wetness periods under 6 hours (MARCHETTI et al., 1976). Severe epidemics only develop after many days of rainfall (Del PONTE et al., 2006). The addition of other influential variables to the disease model would possibly improve estimations of timing to disease onset and development.

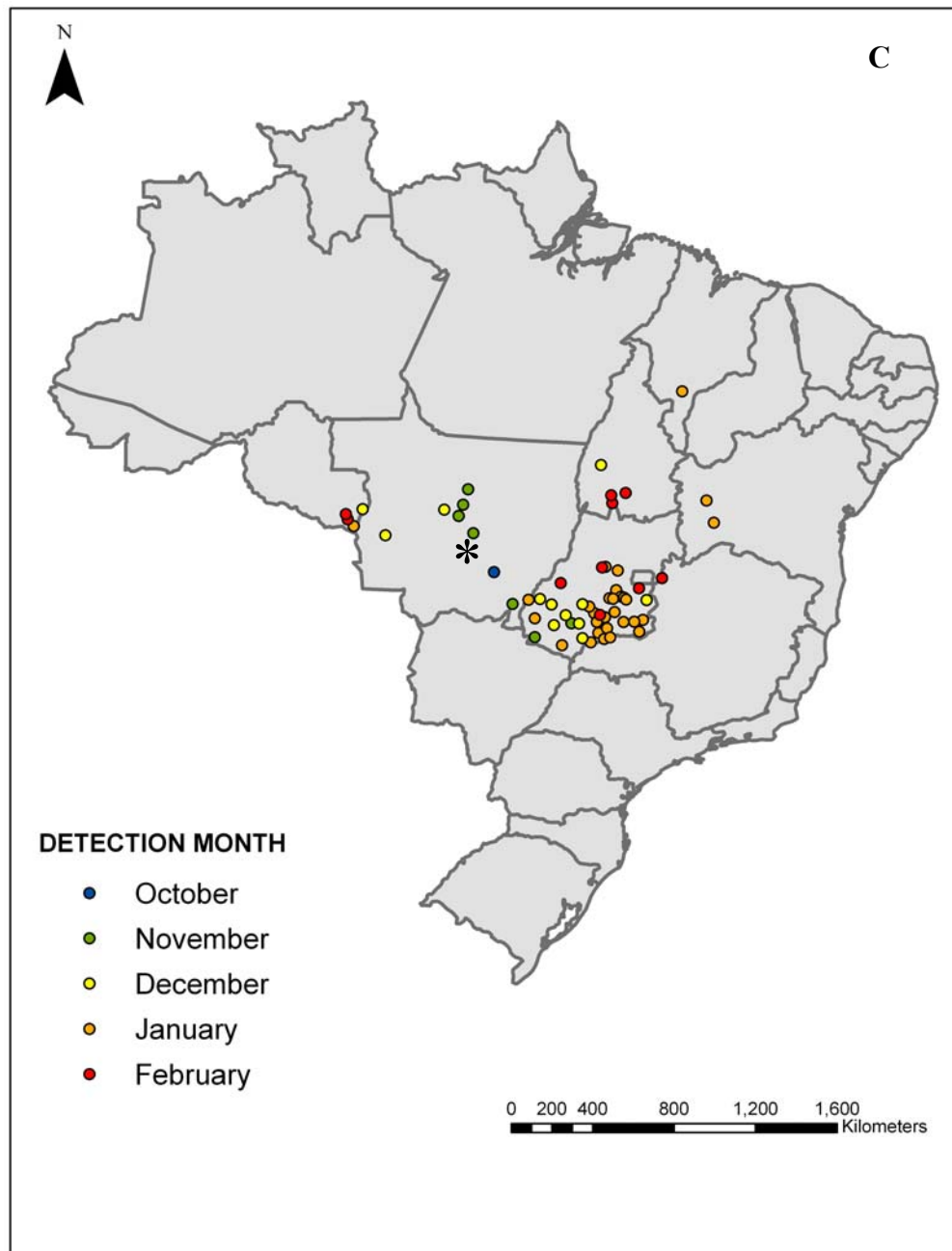
To our knowledge, this was the first attempt to compare ASR epidemic dynamics in Brazil and the United States. Although our study only considered a few of the factors that may affect ASR development, we observed intriguing similarities between the spatial and temporal processes of ASR development in distinctive epidemic cases. Our pioneering results

may support further epidemiological analysis including additional epidemic cases, especially in the United States where soybean rust is still becoming established.

Figures and tables







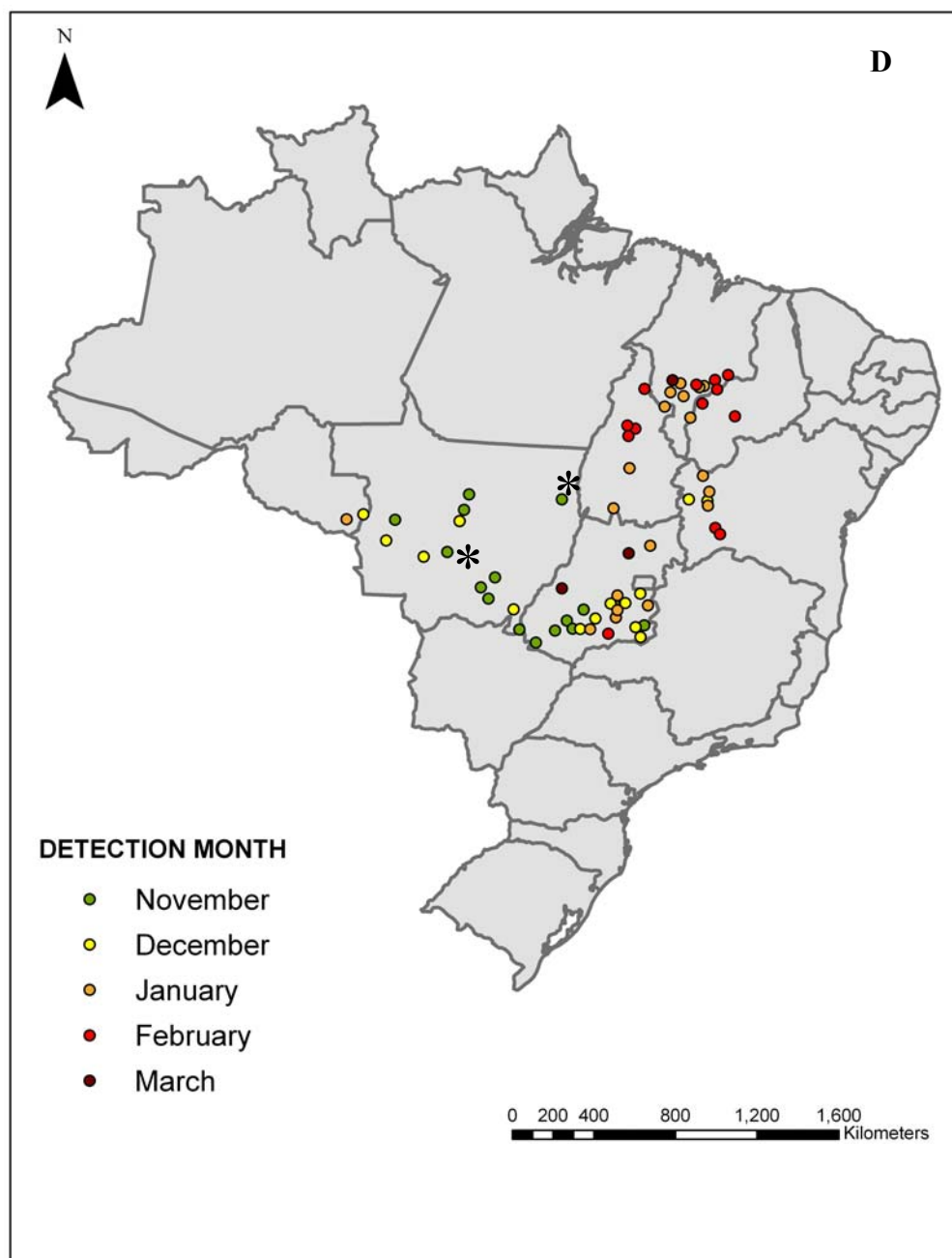
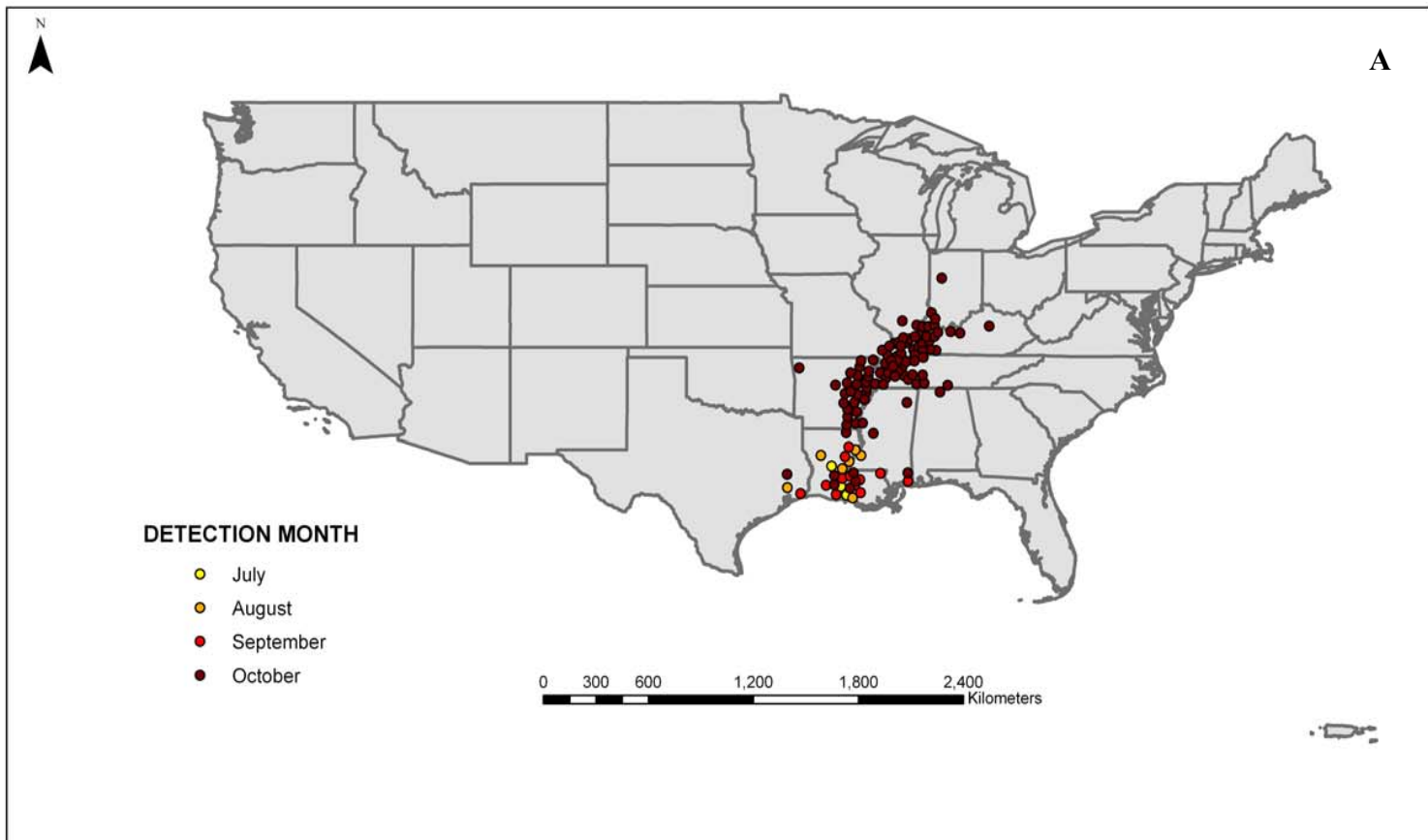


Figure 1: Sites of Asian soybean rust detection in Brazil during the soybean growing season of A) 2003-04; B) 2004-05; C) 2005-06 and D) 2006-07. Stars represent observed overwintering regions in central Brazil. Source: EMBRAPA SOYBEAN, 2007.



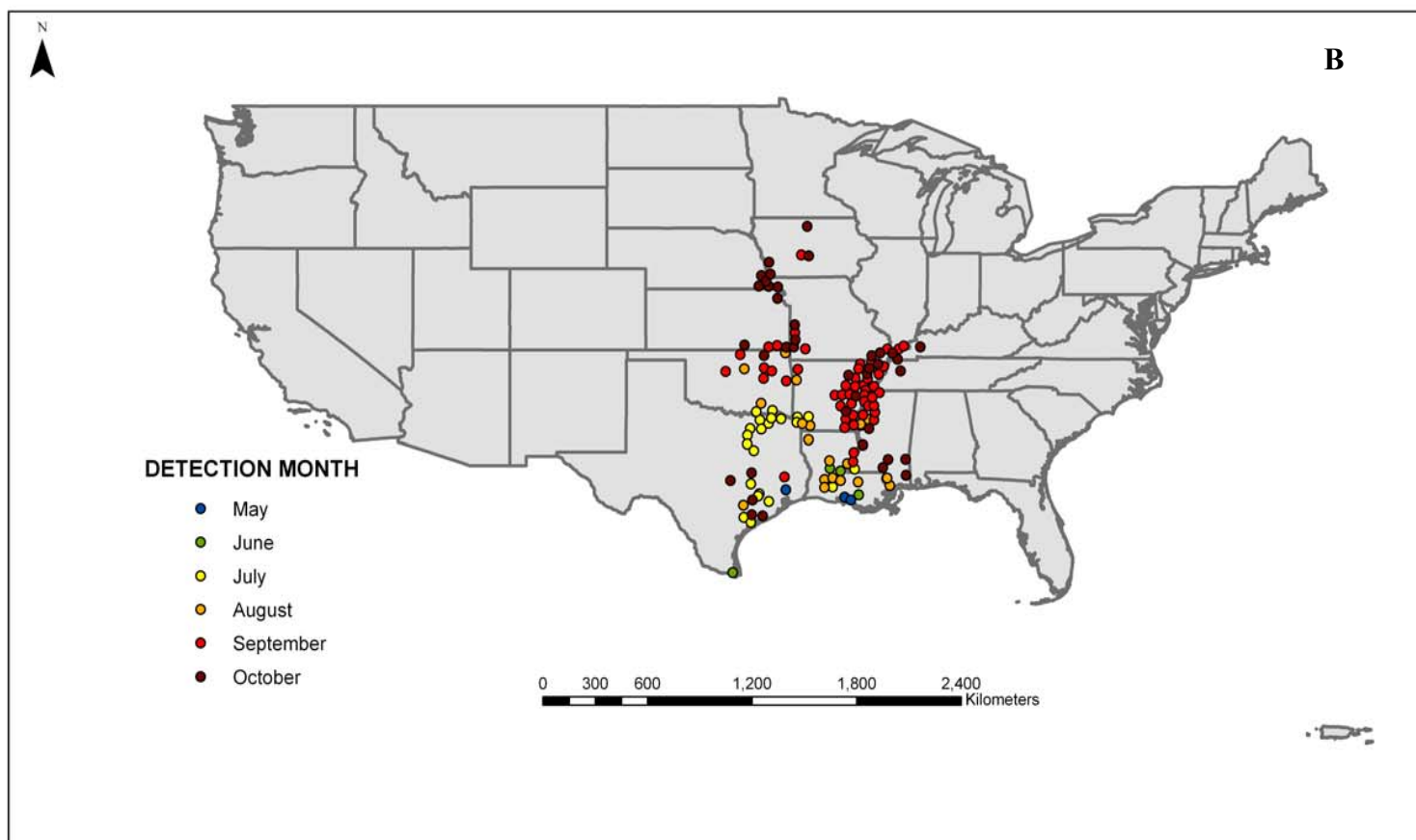
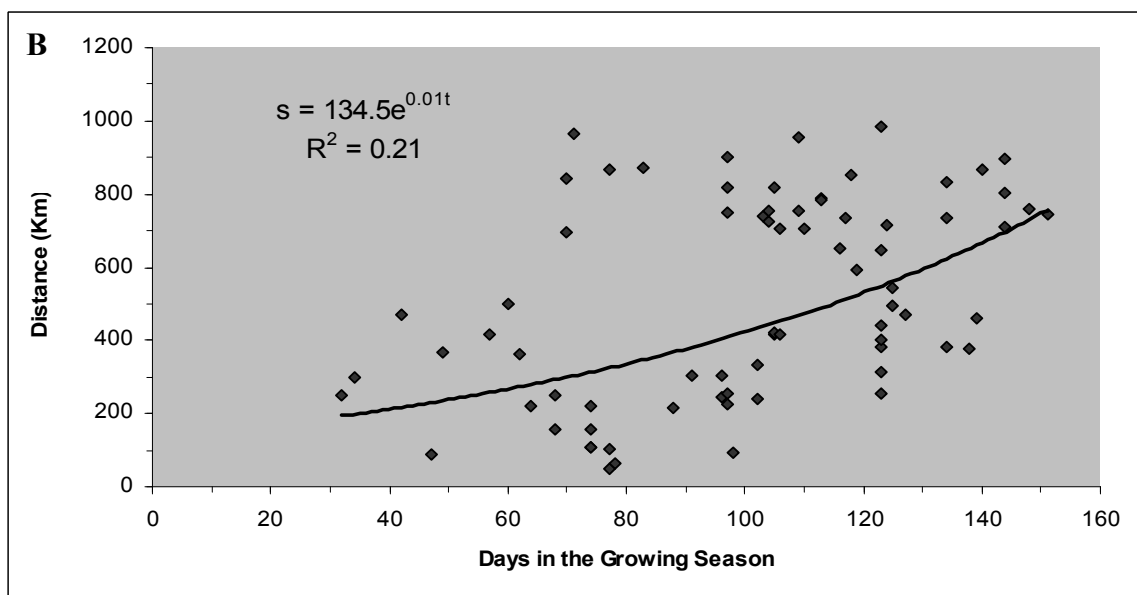
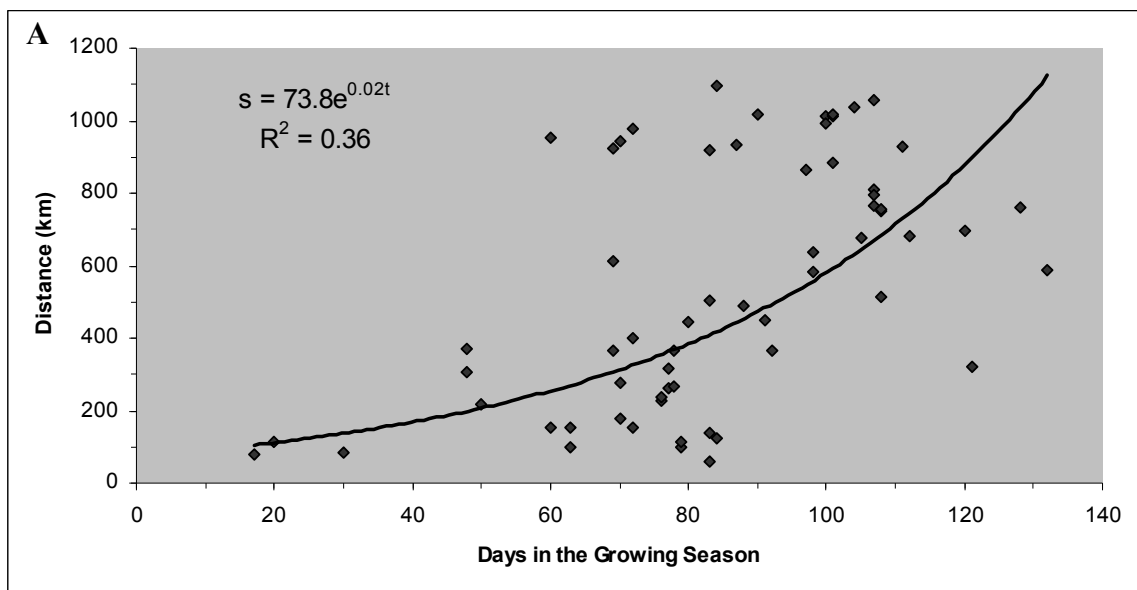


Figure 2: Sites where Asian soybean rust was detected in the central United States during the soybean growing season of A) 2006 and B) 2007 (up to 10 Oct 2007). Source: USDA, 2007.



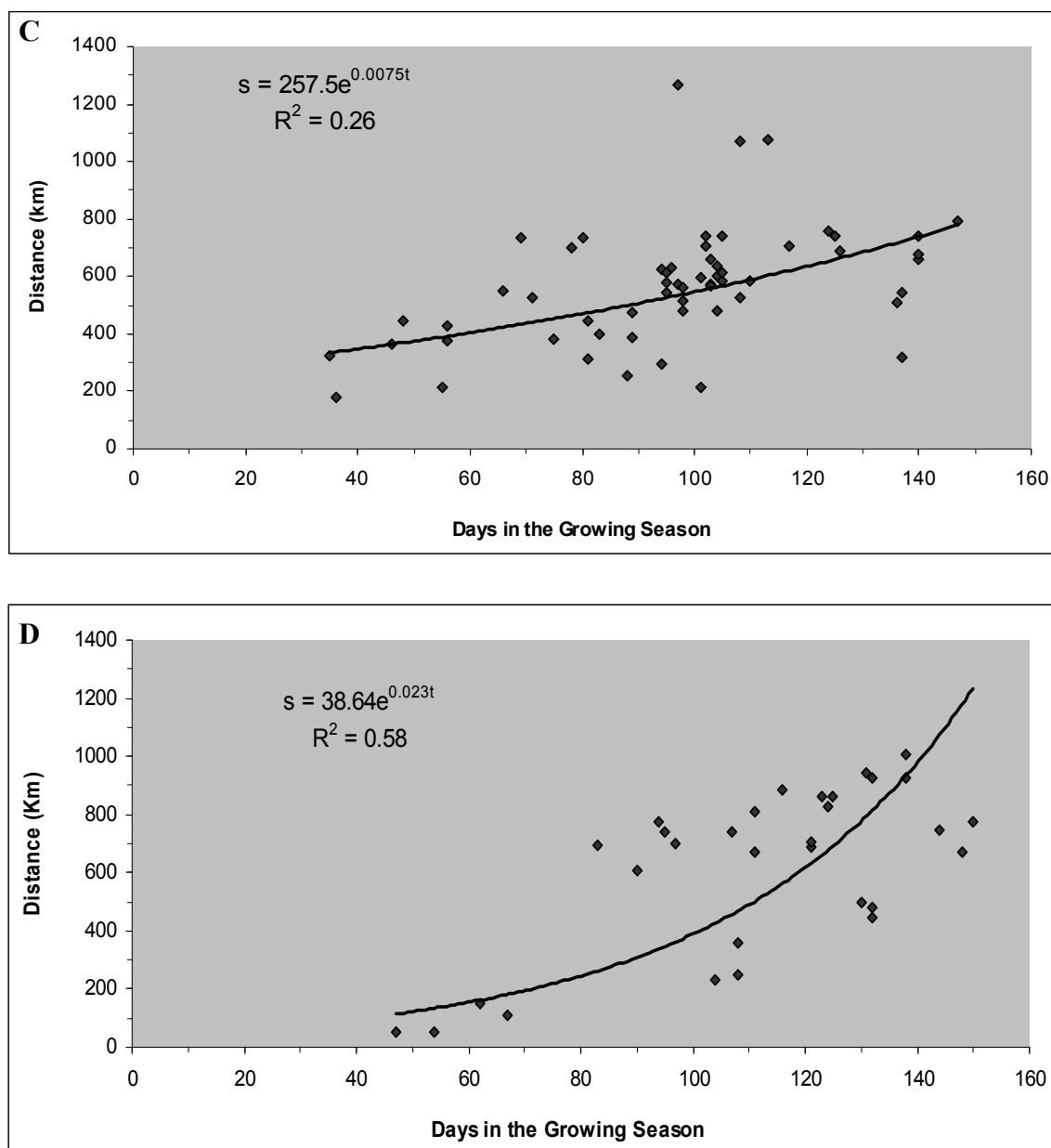


Figure 3: Temporal distribution of the distances where Asian soybean rust was found at detectable levels in north-central Brazil: A) 2003–2004; B) 2004–2005; C) 2005–2006, and D) 2006–2007. Lines represent the solution for the equations derived from exponential regression of the data.

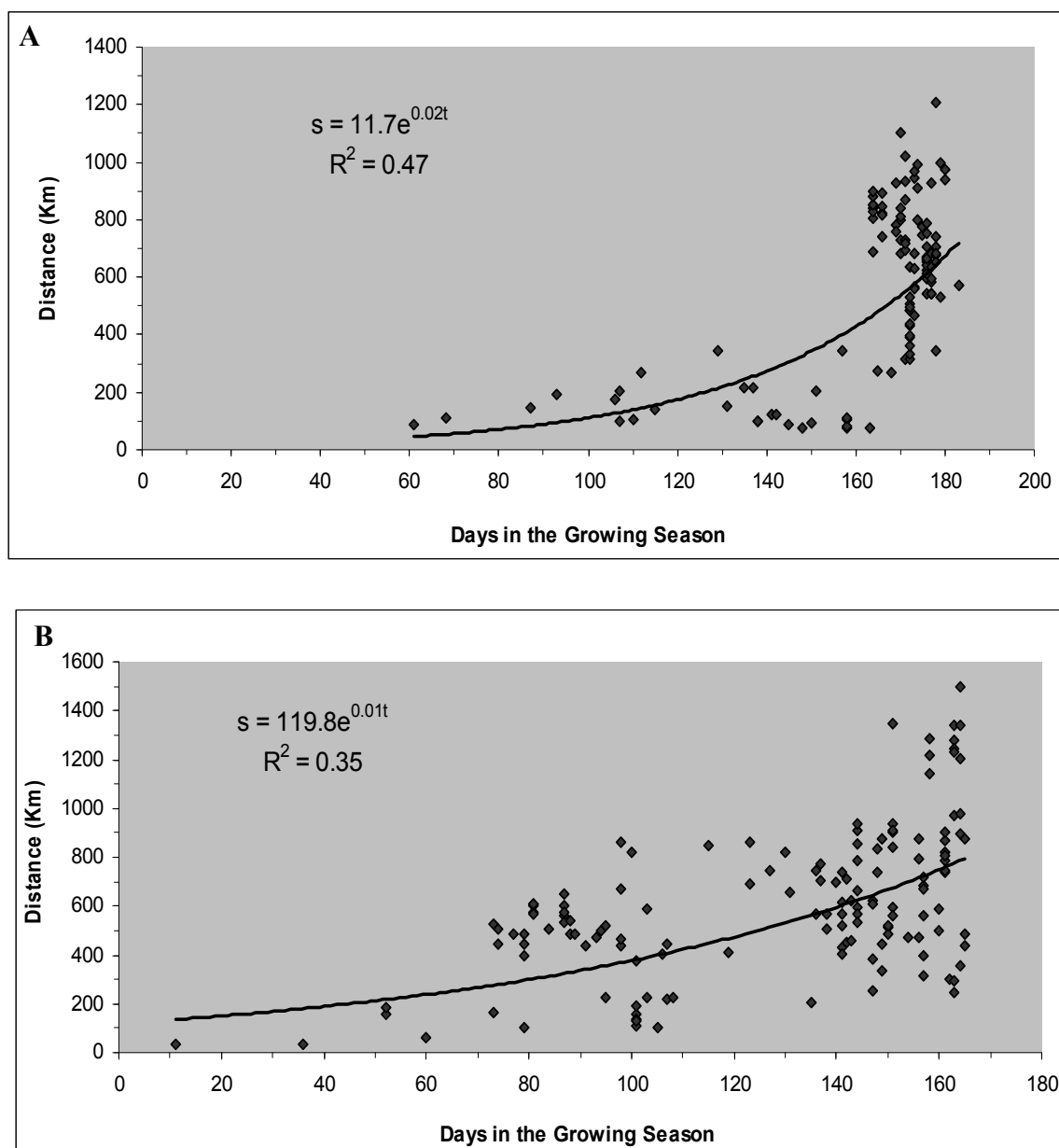
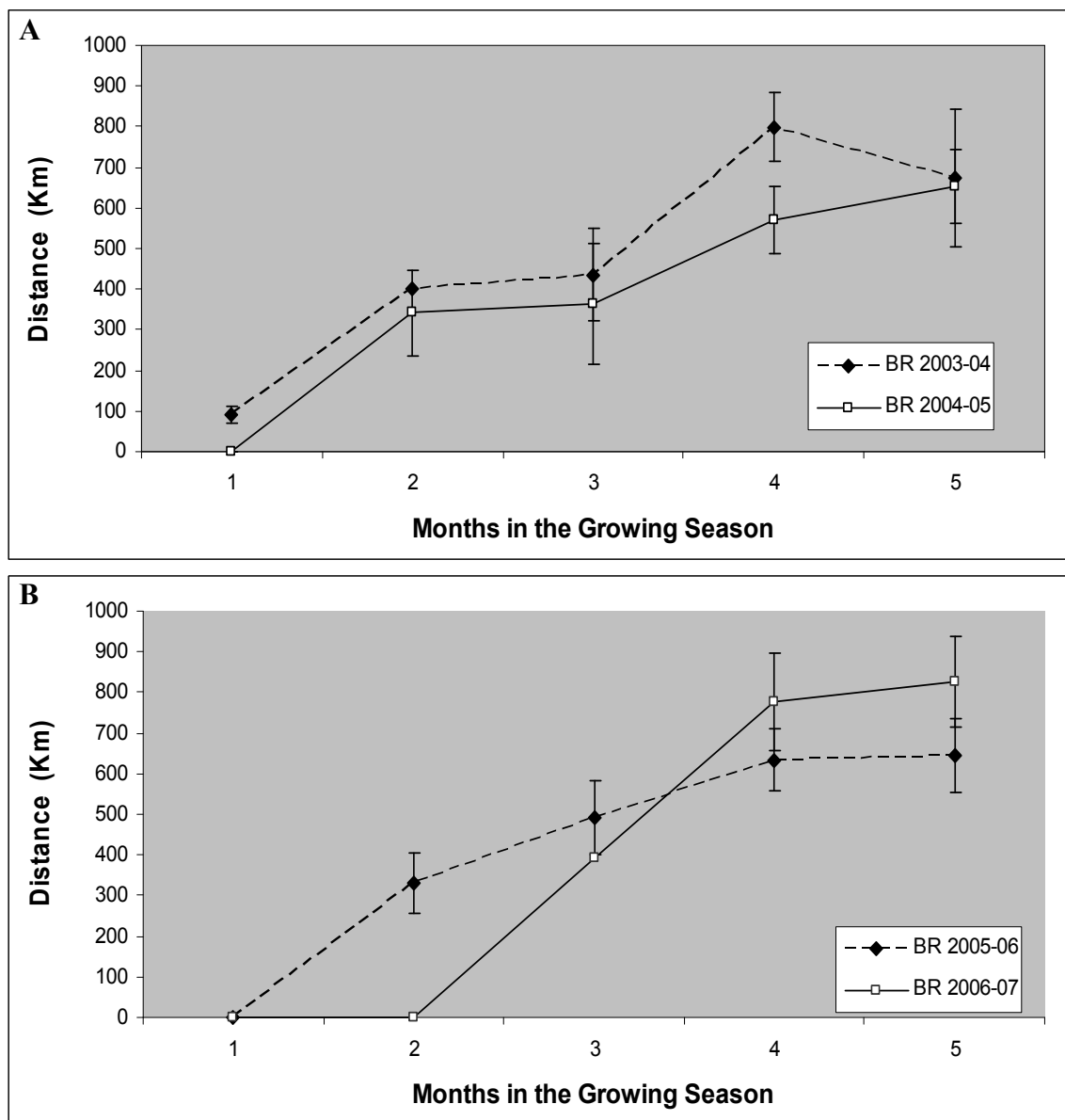


Figure 4: Temporal distribution of the distances where Asian soybean rust was found at detectable levels in the Mississippi Basin of the United States: A) 2006; B) 2007. Lines represent the solution for the equations derived from exponential regression of the data.



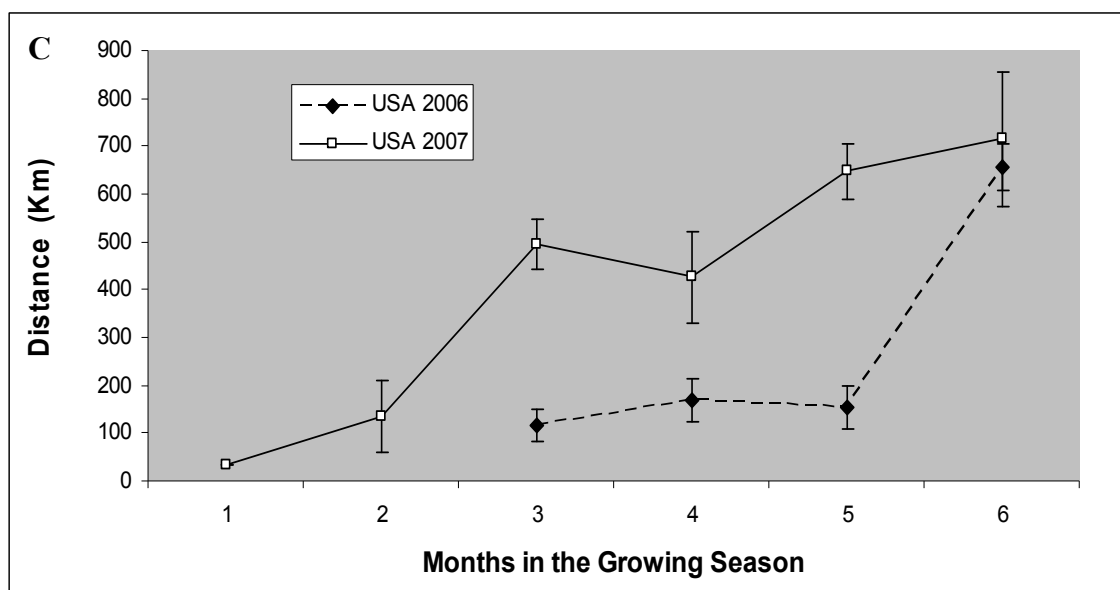
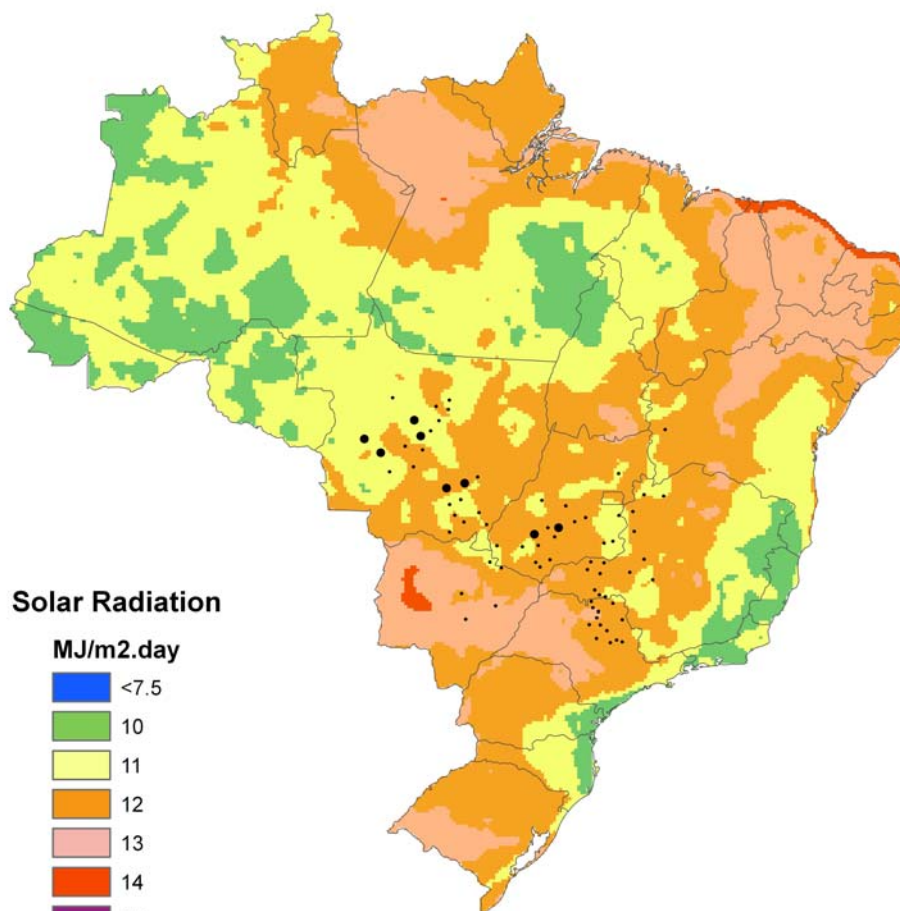


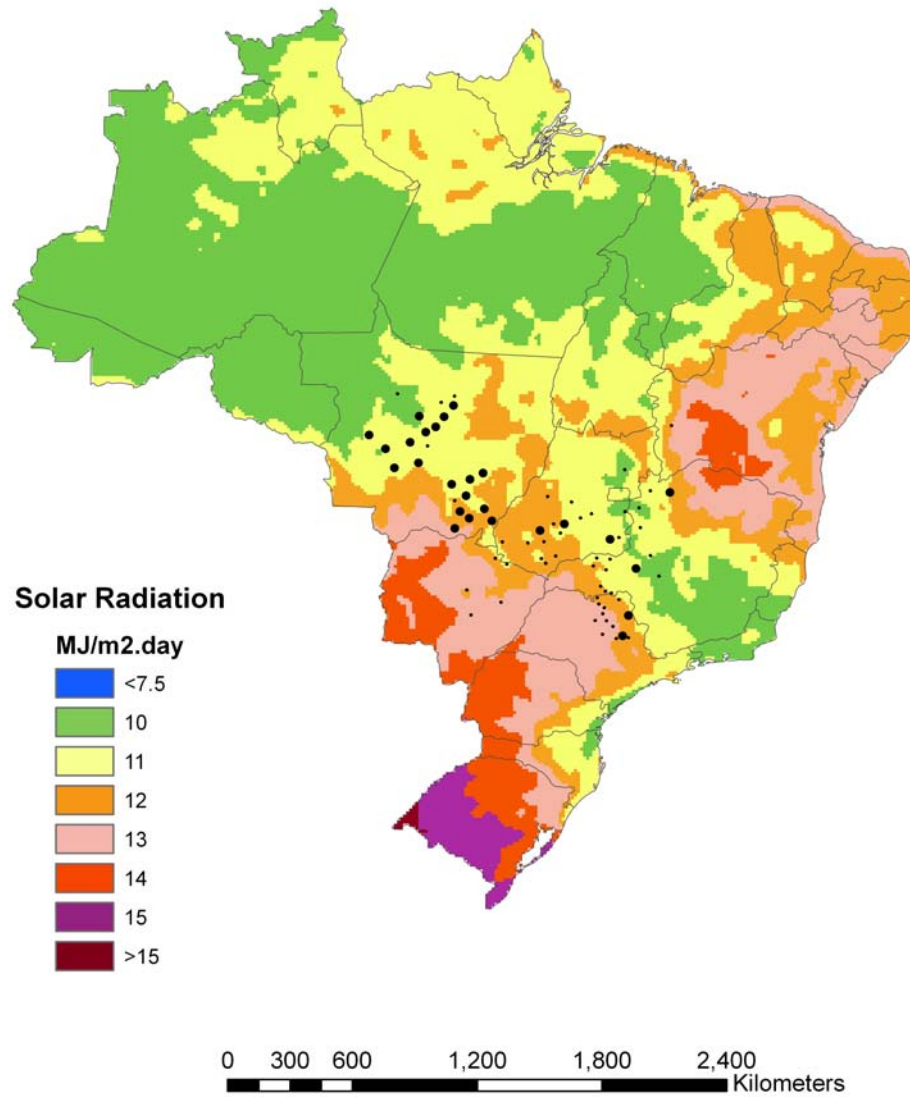
Figure 5: Monthly average distribution of the distances where Asian soybean rust was found at detectable levels in north-central Brazil (A and B) and in the central United States (C). Error bars represent the 95% confidence interval of the mean calculated from the data.



A

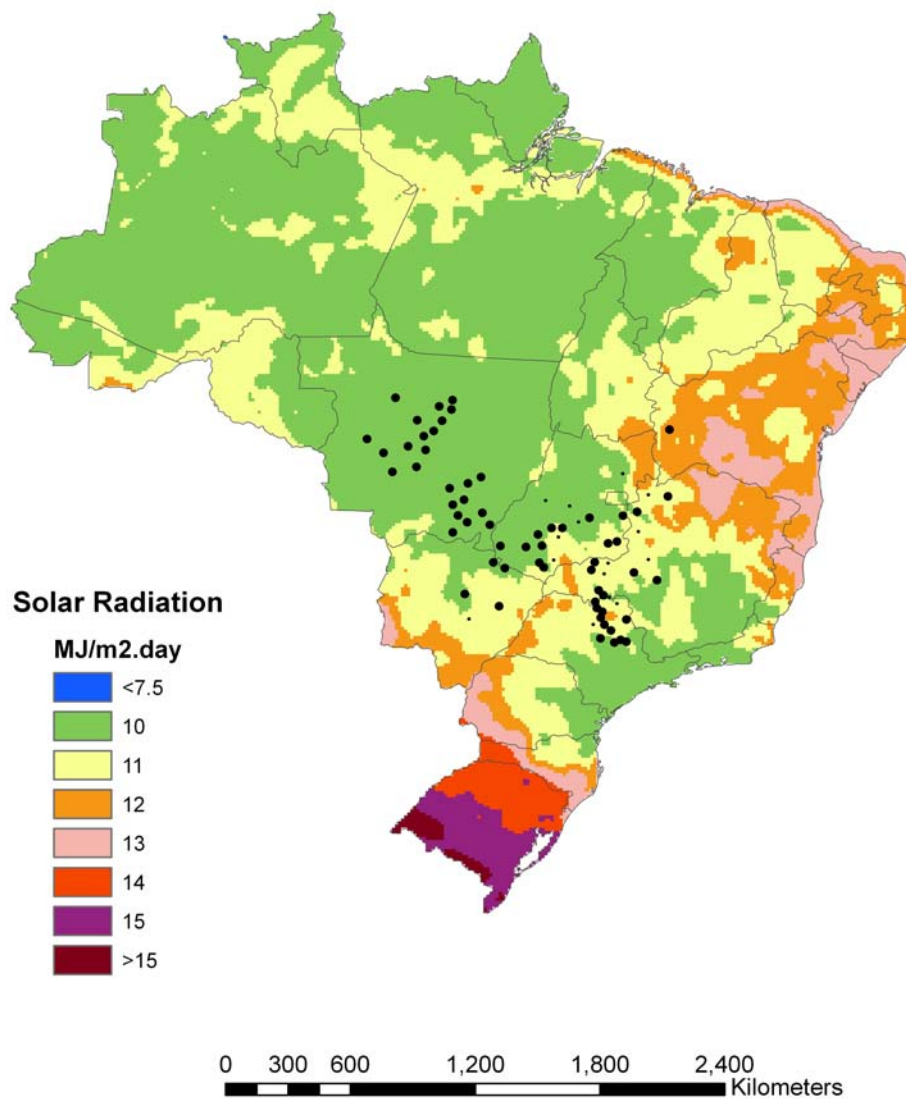


0 300 600 1,200 1,800 2,400 Kilometers

**B**



C



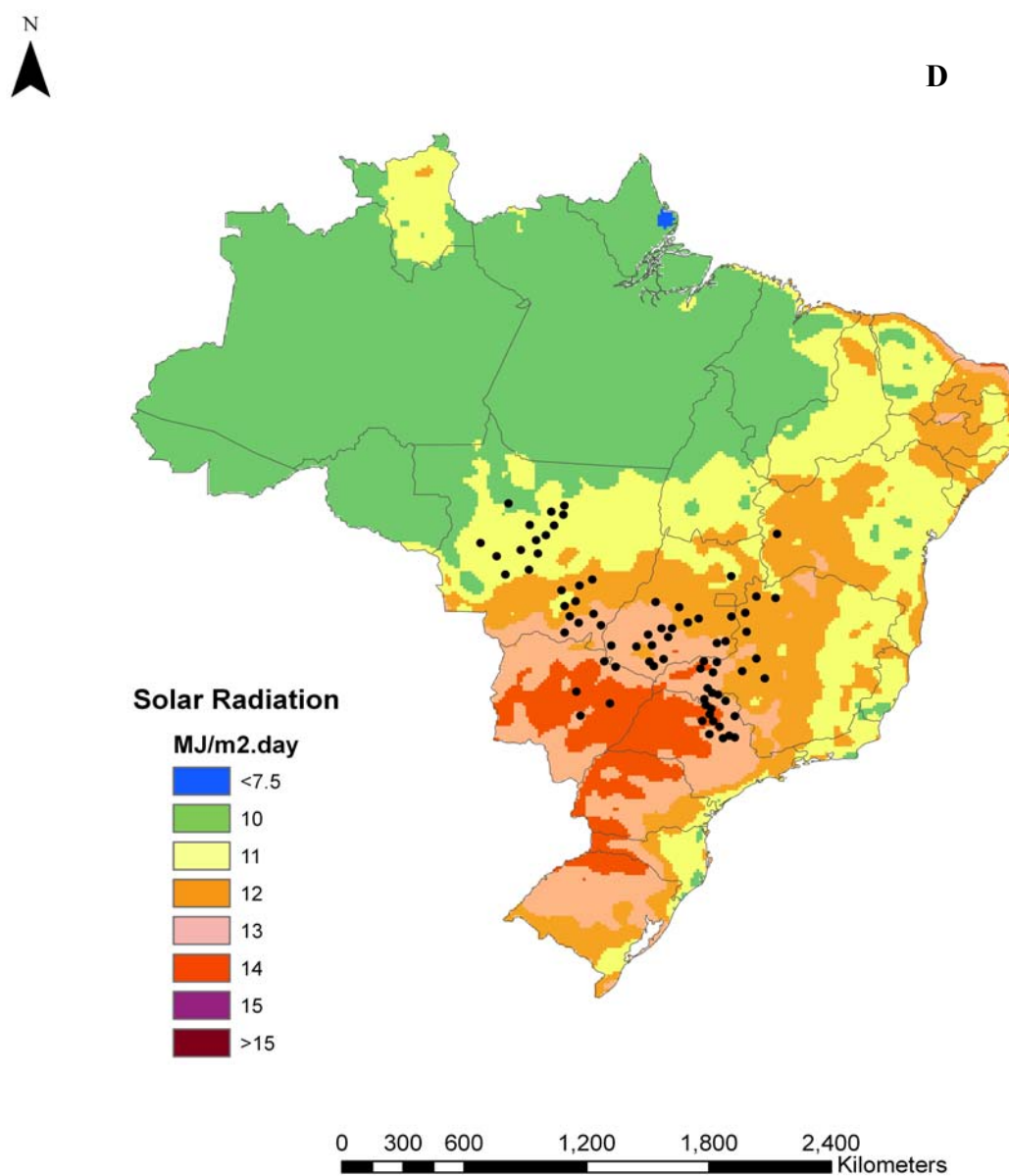
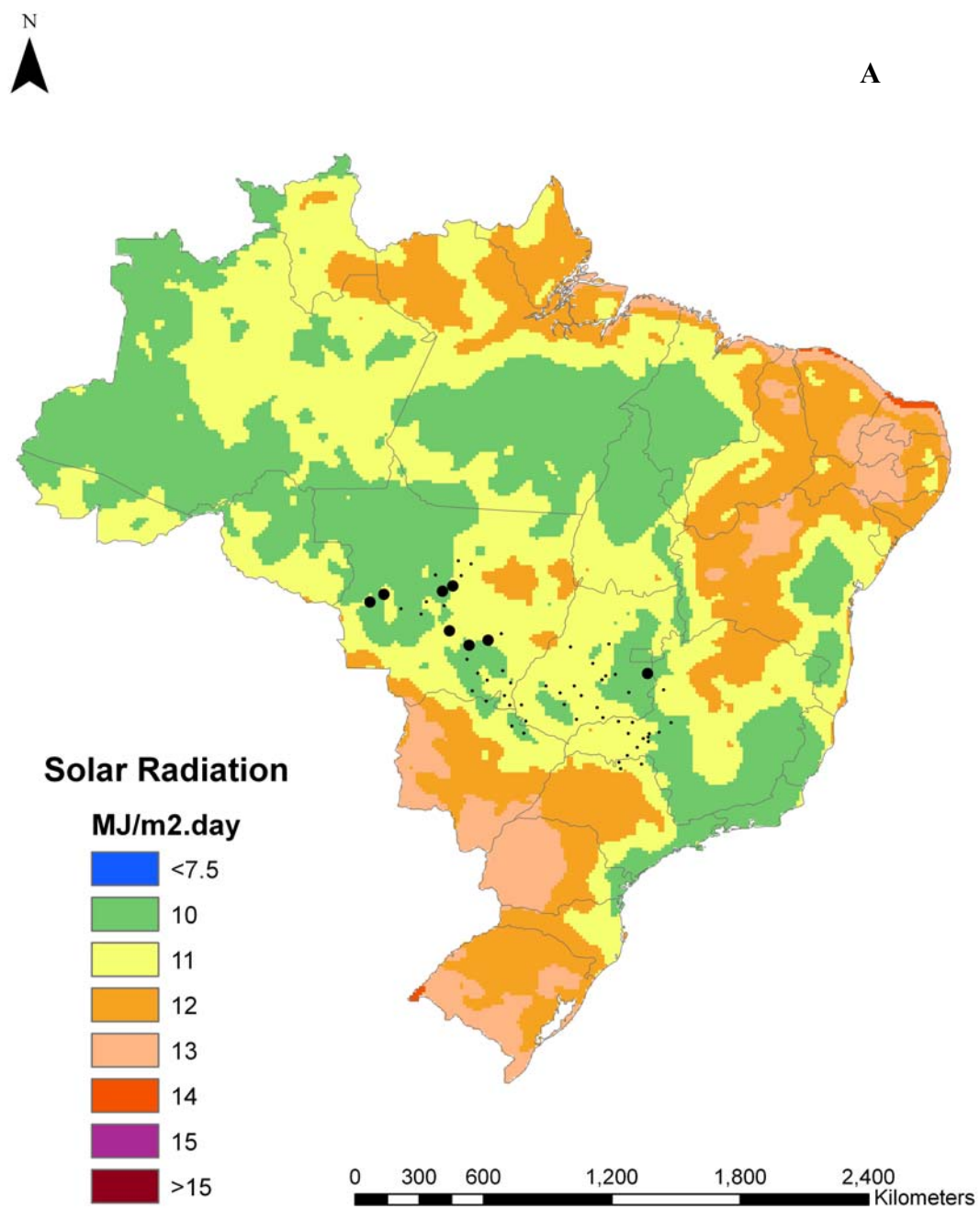
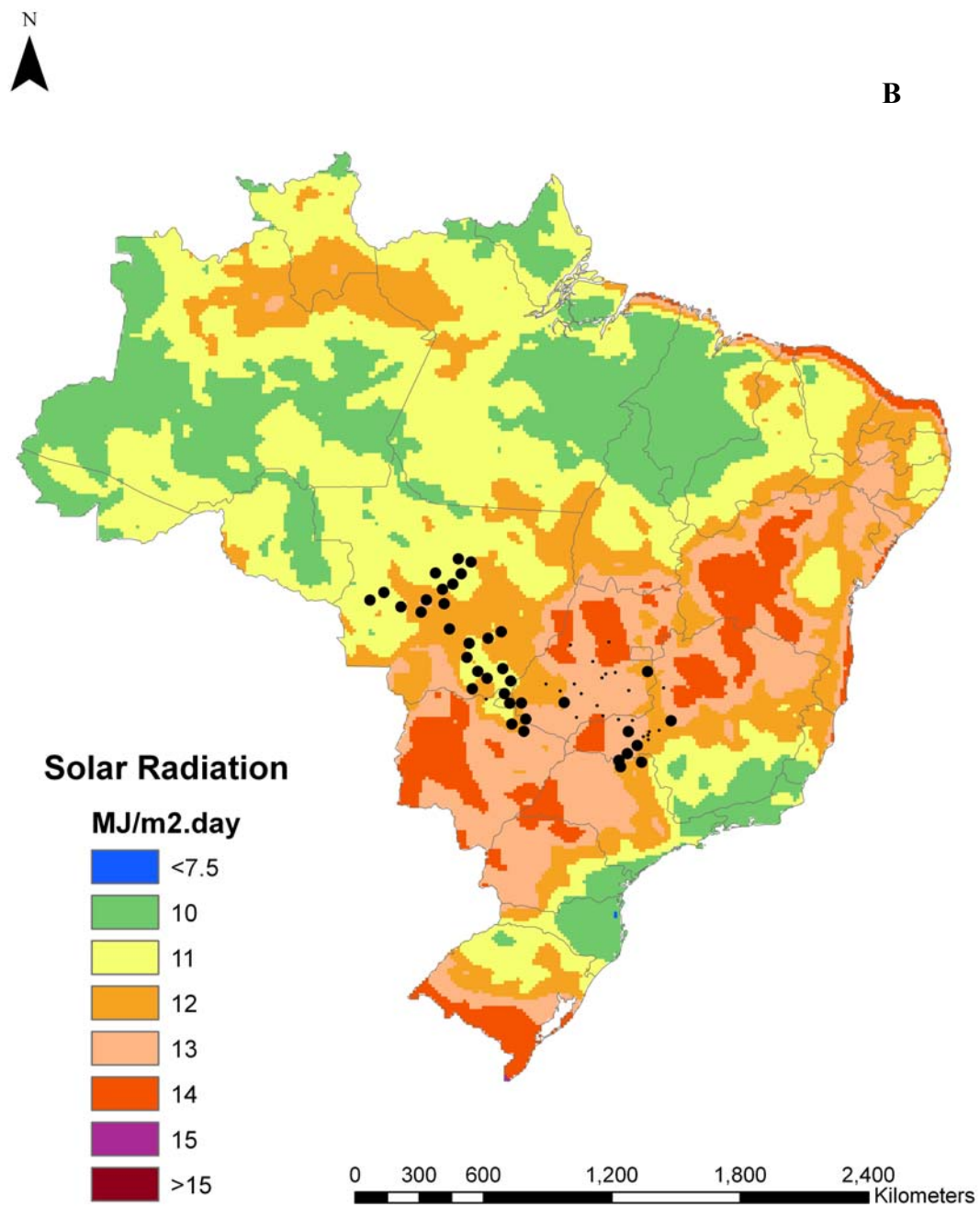
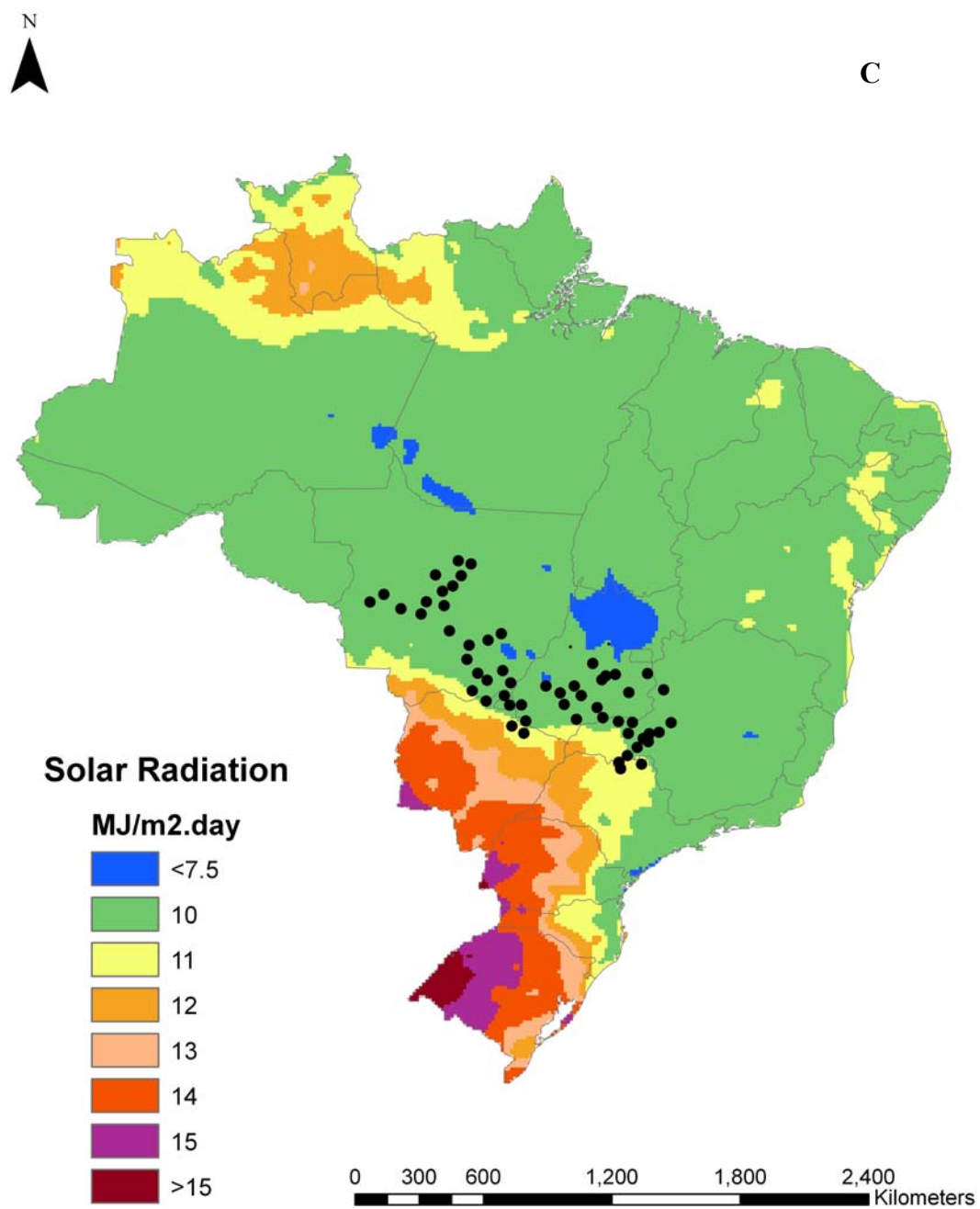


Figure 6: Solar radiation intensity ($\text{MJ.m}^{-2}.\text{day}^{-1}$) estimated in Brazil during the soybean growing season months: A) November-2004 B) December-2004 C) January-2005 and D) February-2005. Large dots represent locations of Asian soybean rust detections up to the graph month and small dots represent locations of later Asian soybean rust detections in the same season. Source: Pentad Matrix GL1.2 (V01), CPTEC/INPE.







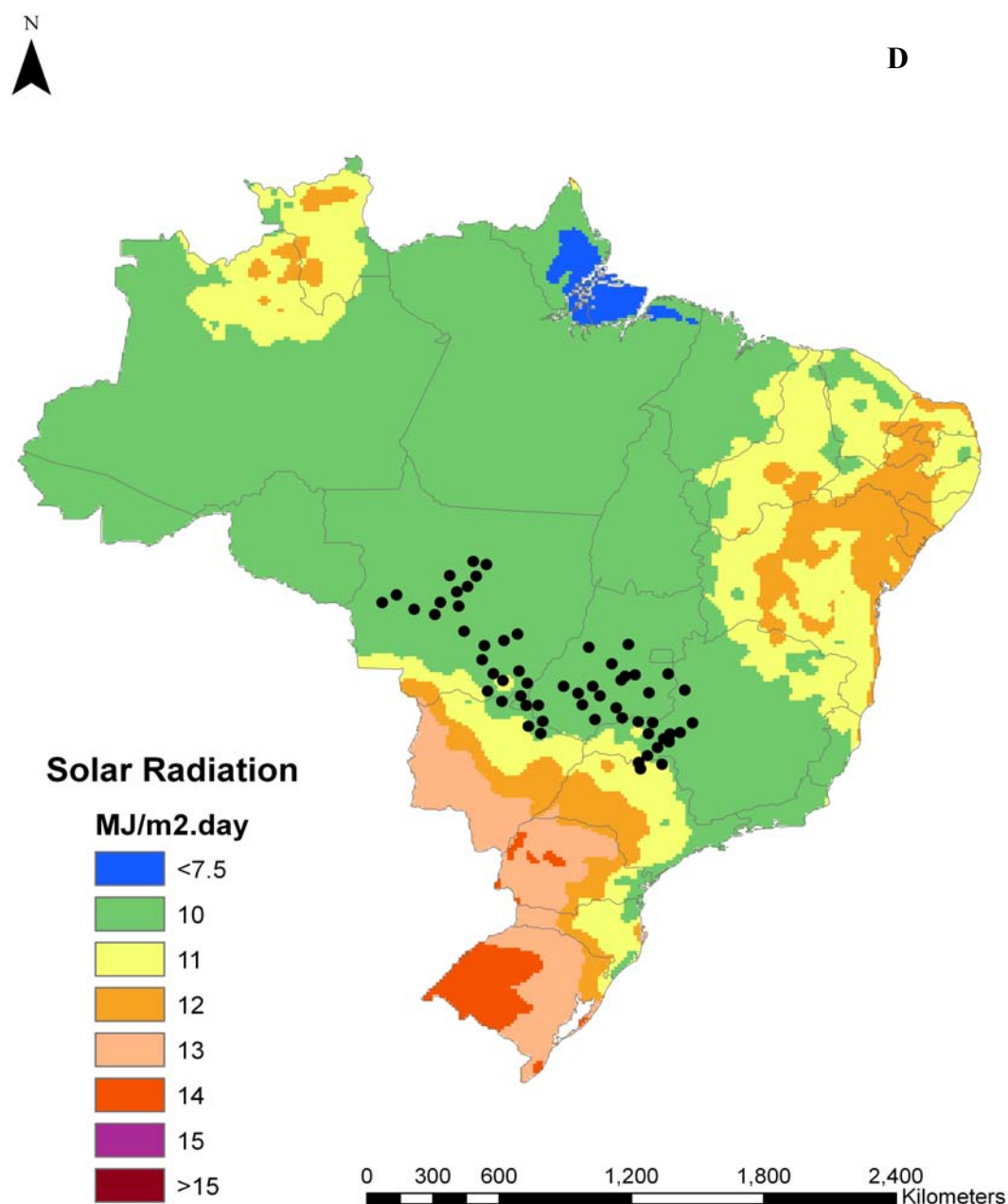
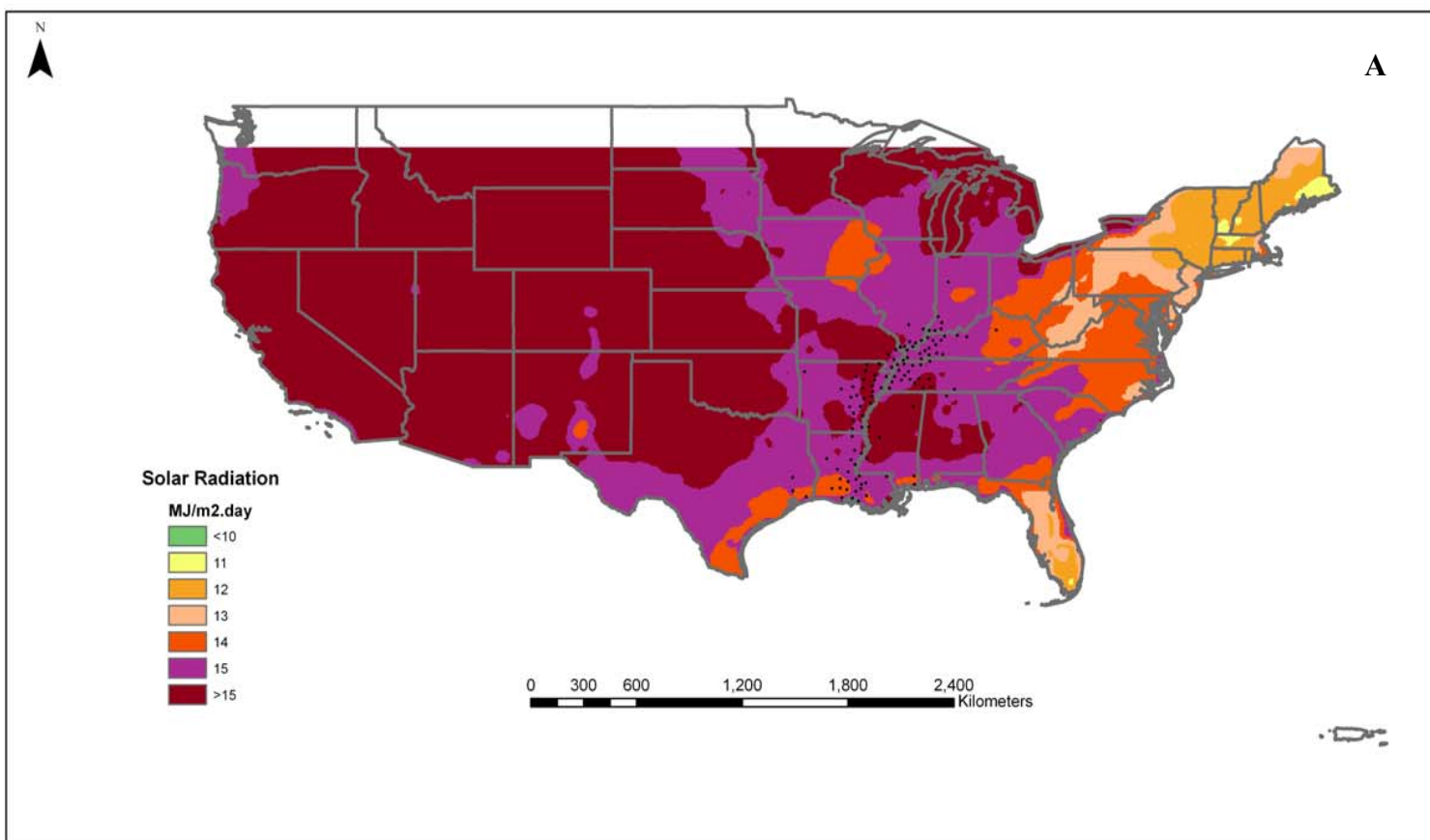
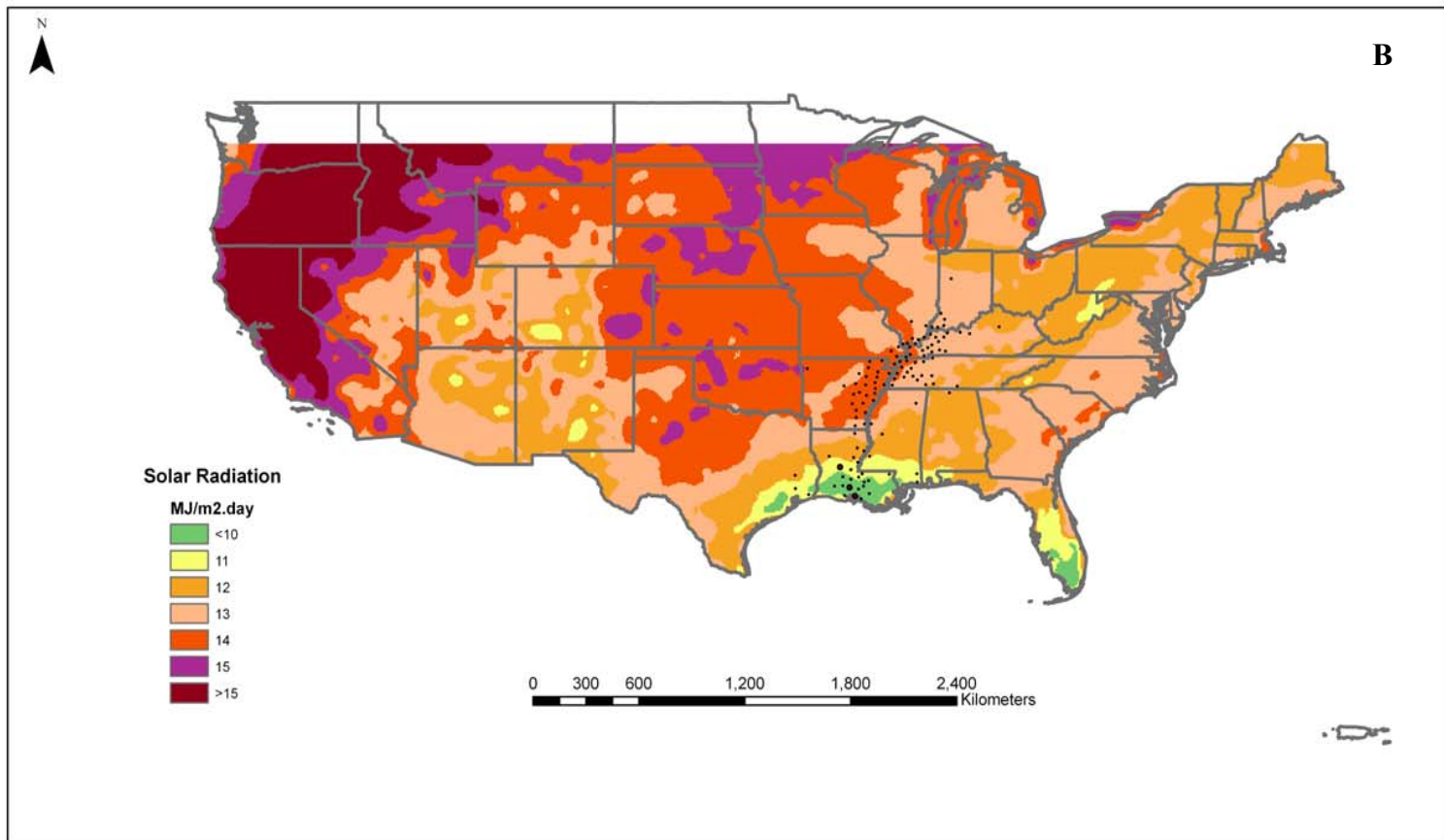
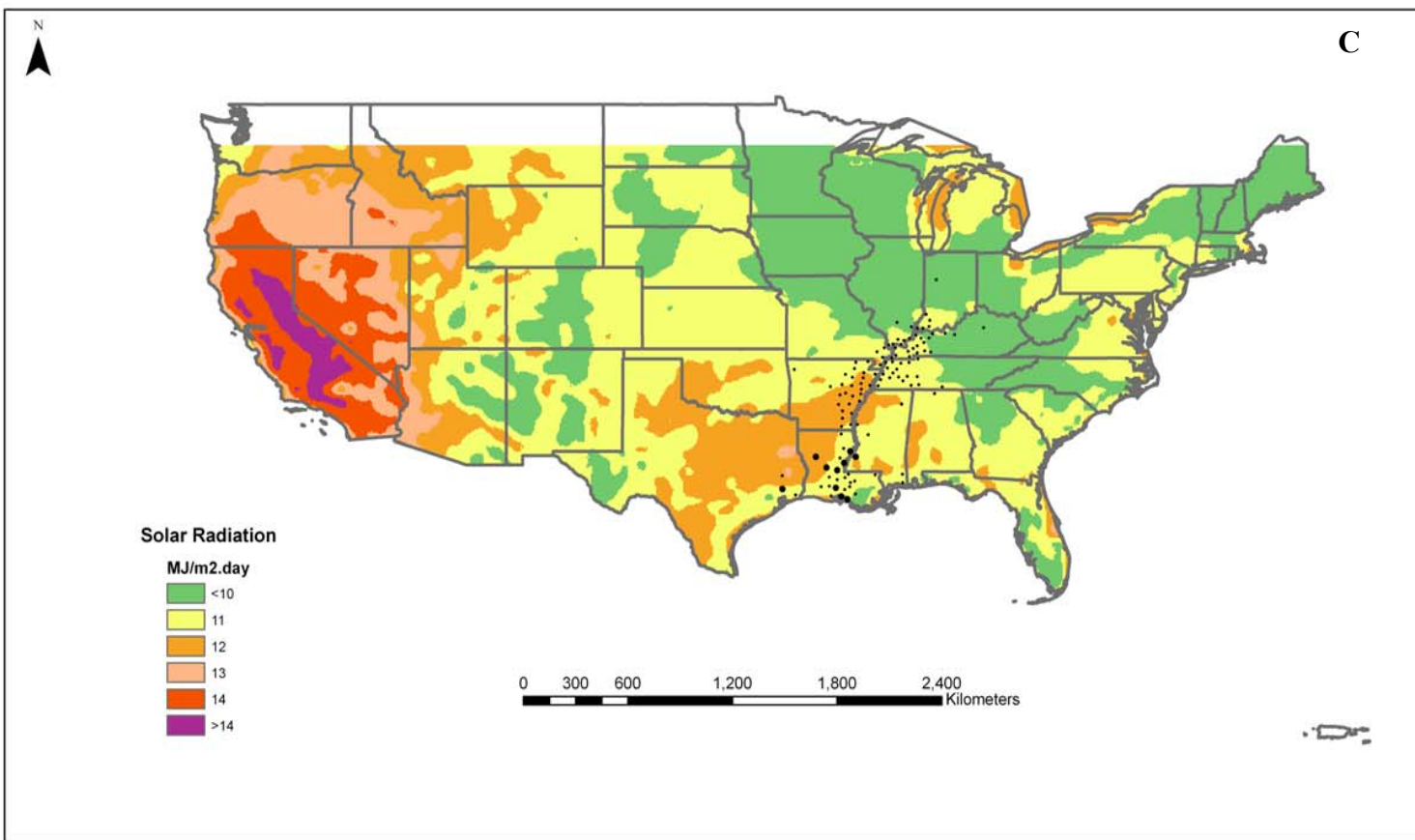


Figure 7: Solar radiation intensity ($\text{MJ.m}^{-2}.\text{day}^{-1}$) estimated in Brazil during the soybean growing season months: A) November-2003 B) December-2003 C) January-2004 and D) February-2004. Large dots represent locations of Asian soybean rust detections up to the graph month and small dots represent locations of later Asian soybean rust detections in the same season. Source: Pentad Matrix GL1.2 (V01), CPTEC/INPE.







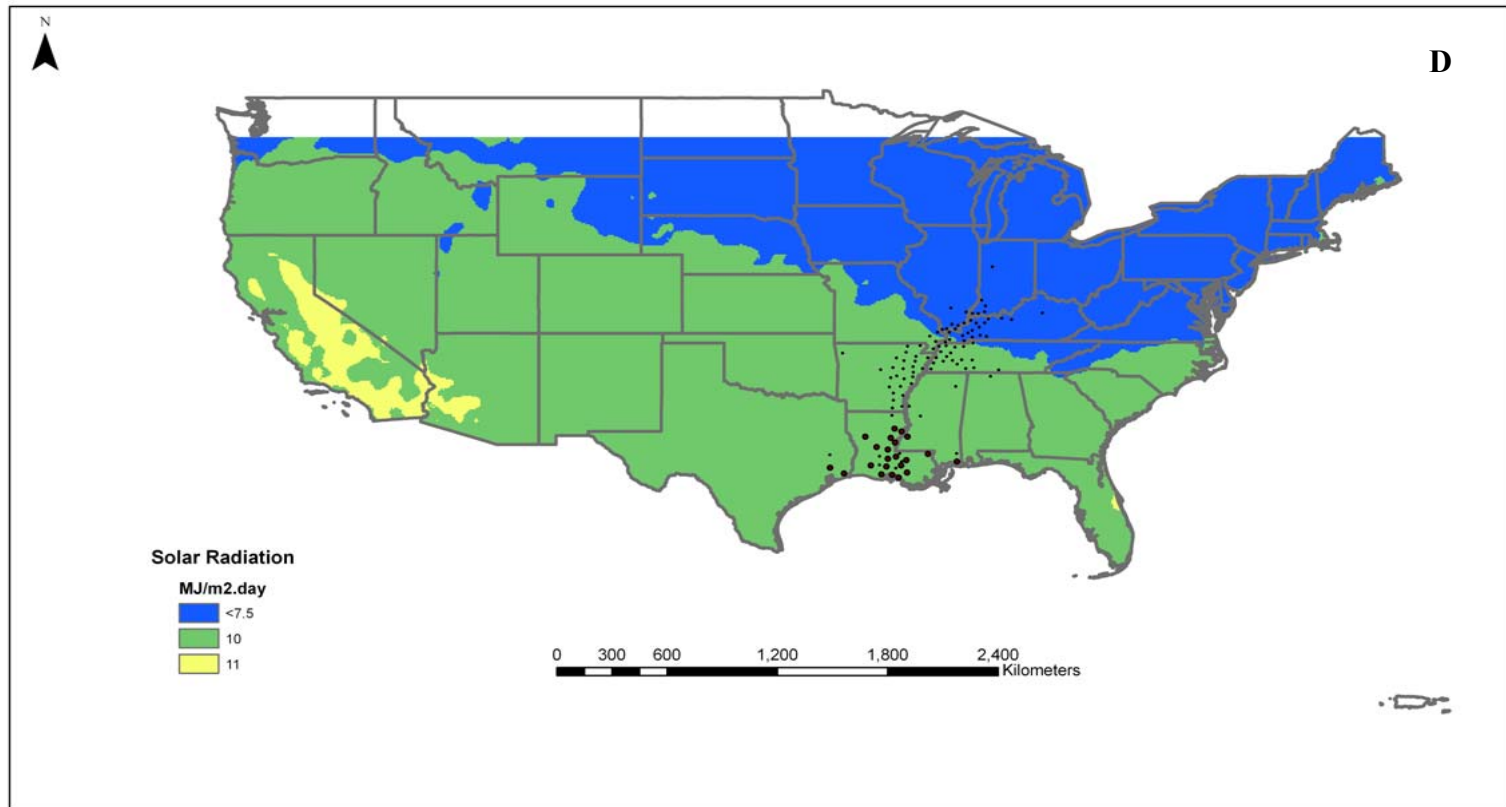


Figure 8: Solar radiation intensity ($\text{MJ.m}^{-2}.\text{day}^{-1}$) estimated in the United States during the soybean growing season months: A) June-2006 B) July -2006 C) August-2006 and D) September-2006. Large dots represent locations of Asian soybean rust detections up to the graph month and small dots represent locations of later Asian soybean rust detections in the same season. Source: Surface Radiation Budget Data, GCIP/GAPP

Table 1: Average estimates of solar radiation intensity ($\text{MJ m}^{-2} \text{ day}^{-1}$) at major soybean regions in Brazil and in the United States during the months corresponding to different soybean growth stages: Brazil (November, December, January, and February) and United States (June, July, August, and September).

	Vegetative	Flowering	Seed Filling	Harvest
Brazil	10.2	11.8	8.6	9.2
2003-04	(0.1) ¹	(0.1)	(0.1)	(0.1)
Brazil	11.3	11.1	10.0	12.1
2004-05	(0.1)	(0.2)	(0.1)	(0.3)
United States	14.8	12.7	10.6	7.91
2006	(0.1)	(0.2)	(0.1)	(0.2)

¹. Values in parenthesis represent the 95% confidence interval of the mean.

Table 2: Estimated Pearson's correlations between distances (km) of Asian soybean rust detection locations; days in the growing season when the disease was detected; and solar radiation intensity at soybean vegetative stage (R_{VG}), flowering stage (R_{FL}), and seed filling stage (R_{SF}).

	Days	Distance	R_{VG}	R_{FL}
Distance	0.33 ¹	-	-	-
R_{VG}	0.86	0.11	-	-
R_{FL}	0.61	0.47	0.55	-
R_{SF}	0.67	0.10	0.77	0.39

¹. All estimates were significant at $P = 0.01$.

Table 3: Estimates of multiple regression analyses of growing season days of Asian soybean rust detected in Brazil and in the United States as a function of distance (km) of disease detection locations and solar radiation intensity at soybean vegetative stage (R_{VG}) and/or flowering stage (R_{FL})^{1,2}

	Estimate	p-value	VIF	R^2	RMSE
Brazil 2003-04				35.01%	19.50
Constant	-94.4	0.17	0		
Distance	0.02	0.03	1.81		
R_{FL}	14.6	0.03	0.81		
Brazil 2004-05				26.16%	25.19
Constant	-131.4	0.11	0		
Distance	0.04	0.0007	1.06		
R_{VG}	18.8	0.0119	1.06		
United States 2006				51.8%	13.02
Constant	58.3	0.0003	0		
Distance	0.02	0.0024	1.06		
R_{FL}	7.77	<0.0001	1.06		

POOLED DATA 1			79.5%	19.54
Constant	-110.3	<0.0001	0	
Distance	0.04	<0.0001	1.01	
R _{VG}	17.25	<0.0001	1.01	
POOLED DATA 2			79.8%	19.4
Constant	-131.05	<0.0001	0	
Distance	0.03	<0.0001	1.35	
R _{VG}	16.50	<0.0001	1.50	
R _{FL}	2.77	0.076	1.92	

- ^{1.} VIF = variance inflator factor.
- ^{2.} RMSE = root mean square error.

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CHAPTER 5: GENERAL CONCLUSIONS

Asian soybean rust, caused by *Phakopsora pachyrhizi*, has been reported to cause severe outbreaks resulting in high yield losses in major soybean-producing regions. For this reason, high risk of yield losses is usually assumed, depending on disease onset in most regions. However, disease epidemic patterns vary greatly according to location and season. The occurrence of this disease is influenced by environmental factors, and frequent occurrence of favorable conditions results in severe disease outbreaks.

Field observations have suggested that soybean rust develops more rapidly in the shade. The disease is usually found on lower leaves of closed the soybean canopy and on kudzu vines growing under trees. Among other factors such as reduced temperature and increased air moisture, reduced radiation intensity is the one that is most evidently observed in the shade. In addition, light reportedly inhibits *P. pachyrhizi* development, reducing germination rate and germ tube growth. However, further implications of sunlight on disease epidemiology are still unclear.

This thesis includes three studies. In the first study, we compared soybean rust incidence and severity in different sunlight regimes. We used shade cloth to simulate different levels of shade, but variations of temperature and moisture were controlled among shade treatments. We also simulated shade duration by removing inoculated soybean plants from the shade at different time intervals. We consistently observed greater soybean rust incidence and severity in the shade treatments compared to no-shade treatments. A minimum period of 2 days in the shade resulted in greater disease incidence on inoculated soybean

plants. In our studies, there was no evidence that direct sunlight reduced the rates of uredinospore germination and appressoria and penetration peg formation. However, disease incidence and severity were consistently greater in the shade. In general, disease incidence was reduced at solar radiation intensity greater than $10 \text{ MJ m}^{-2} \text{ day}^{-1}$.

In the second study, soybean rust epidemics were examined using cloud cover as a independent variable to represent the shading effect on regional disease development. Temporal disease development was estimated starting at the first disease detection dates in different years and different regions in Brazil and South Africa, which had a total of 30 unique soybean rust epidemic events. Cloud cover frequency was found to be an accurate predictor of soybean rust development on a regional scale in Brazil and South Africa. Regions with at least 18 cloudy days in a growing season usually had more severe epidemics compared to regions with less than 8 cloudy days.

In the third study, the rates and patterns of soybean rust expansion in a region were estimated during two soybean growing seasons in the United States and four seasons in Brazil. The timing of disease onset was correlated to the distance of disease site from inoculum source regions and solar radiation intensity patterns. We observed that soybean rust epidemics expanded to similar distances in Brazil and the United States following non-wavelike exponential patterns. Timing for disease detection increased at larger distances from inoculum sources and at locations exhibiting higher solar radiation intensity in both countries.

In summary, our results suggested that sunlight affects soybean rust establishment and epidemiology. Disease incidence and severity were reduced on inoculated plants in full

sunlight compared to those in shade. Severe epidemics were often observed in regions with extended period of cloud coverage. Finally, disease onset was delayed at similar distances from inoculum source regions receiving greater sunlight intensity.

Although many studies have been conducted in the past 30 years on different aspects of soybean rust, the disease epidemic dynamics are still under investigation. To our knowledge, our studies were the first in quantifying the relationship between Asian soybean rust development and solar radiation patterns. Further, our simulation model estimated temporal disease progress based on cloud coverage conditions, which is a major shading factor on a regional scale in Brazil and South Africa. Finally, we observed that disease fronts move at similar patterns in Brazil and the United States and that high intensity solar radiation during soybean reproductive stages were associated with a delay in Asian soybean rust onset.

Our results should support further investigations of the relationship between Asian soybean rust epidemiology and solar radiation. Also, our cloud cover-based model can be used to assess risks of severe disease outbreaks based on historical weather data at different locations. Finally, our comparative studies determined common aspects of disease epidemics in different countries, which should serve as a guideline to compare the potential of adopting similar strategies for disease predictions and subsequent disease management.